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ON THE CLARIFICATION OF LARVAL TUNA IDENTIFICATION PARTICULARLY IN THE GENUS *Thunnus*

WALTER M. MATSUMOTO,[1] ELBERT H. AHLSTROM,[2] S. JONES,[3]
WITOLD L. KLAWE,[4] WILLIAM J. RICHARDS,[5] AND SHOJI UEYANAGI[6]

ABSTRACT

A Larval Tuna Identification Workshop was held at the Bureau of Commercial Fisheries Biological Laboratory (now the National Marine Fisheries Service, Southwest Fisheries Center), Honolulu, Hawaii, on March 2-6, 1970, to resolve conflicting views on the identification of larvae of *Thunnus alalunga* and *T. albacares* and to clarify the status of larval identification of other *Thunnus* species.

The identification of *T. alalunga* (Yabe and Ueyanagi, 1962), *T. albacares* (Matsumoto, 1958), *T. obesus* (Matsumoto, 1962), and *T. thynnus* (Yabe, Ueyanagi, and Watanabe, 1966) was agreed upon as correct, except that the description of *T. albacares* should include the appearance of black pigmentation at the tip of the lower jaw when the larva attains a length of about 4.5 mm SL and that the lower size limit of reliable identification of *T. alalunga* be set at about 4.5 mm SL until further studies indicate more precisely whether the black pigmentation at the tip of the lower jaw in *T. albacares* appears earlier. There was no difference in appearance of *T. thynnus* larvae from the Atlantic and Indo-Pacific Oceans. The identification of *T. tonggol* and *T. maccoyii* larvae was not conclusive. The larvae of *T. atlanticus* required further study.

The workshop further concurred that juveniles (13-200 mm SL) of several species of *Thunnus* may be separated by internal and external characters: *T. atlanticus* by vertebral count, *T. alalunga* by shape of first elongate haemal spine and arrangement of pterygiophores of the second dorsal fin relative to two adjacent neural spines, and *T. thynnus* by configuration of lateral line and arrangement of pterygiophores of the second dorsal fin; and that juveniles of *T. obesus* and *T. albacares* may be separated from the previous three species by arrangement of pterygiophores of the second dorsal fin, but not from each other.

The proper identification of larval tunas has been a perplexing and difficult problem for many years. Although progress in the past two decades has resulted in agreement on the identification of larvae of a number of species (*Katsuwonus pelamis, Euthynnus alletteratus, E. affinis, E. lineatus, Thunnus thynnus, T. obesus,* and *Auxis* spp.), there is still some disagreement and confusion on the identity and description of *T. alalunga* and *T. albacares*. At the present time there are two different descriptions given for *T. alalunga* (Matsumoto, 1962; Yabe and Ueyanagi, 1962). The identity of other tunas, such as *T. tonggol, T. maccoyii,* and *T. atlanticus*, has yet to be confirmed or resolved.

One of the chief problems in larval tuna identification is the difficulty in obtaining good series of larvae for study. Tuna larvae are seldom taken in sufficient numbers by the usual collecting methods, and individuals over 10 mm standard length (SL) are taken rather infrequently. Additionally, although the young of a number of tuna species are found together in many parts of the ocean, some species are localized in certain areas. Consequently, it is extremely difficult for workers in different parts of the world to have

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at hand a complete series of larvae of more than two to four species.

In an attempt to resolve the conflicting views on *T. alalunga* and to review the identification of larvae of other species of tunas, a Larval Tuna Identification Workshop was held at the Bureau of Commercial Fisheries (BCF) Biological Laboratory (now the National Marine Fisheries Service, Southwest Fisheries Center), Honolulu, Hawaii, on March 2-6, 1970. The workshop also afforded an opportunity to workers specializing on larval tuna identification to assemble specimens of the various species of tunas and to examine these together. The procedure followed at the workshop was (1) to summarize the status of larval tuna identification to date by species and (2) to evaluate the identifying characters by examining larval specimens. As time permitted, the status of juvenile tuna identification was also examined.

The participants included:

Mr. Walter M. Matsumoto, Convenor
Dr. Elbert H. Ahlstrom, Advisor
Dr. Santhappan Jones
Mr. Witold L. Klawe
Dr. William J. Richards
Dr. Shoji Ueyanagi

Dr. Jean-Yves Le Gall of the Centre Océanologique de Bretagne, Brest, France, attended the workshop as an observer.

The sessions were conducted informally with a summary of the present status of larval tuna identification, including recent developments, followed by evaluation of the various characters that could be relied upon for positive identification. Most of the sessions were devoted to direct examination of larval specimens of the various species and discussions of unpublished data offered by participants.

This report summarizes the proceedings and results of the workshop.

RECENT DEVELOPMENTS IN THE IDENTITY OF *Thunnus alalunga*

Two differing versions of the identity and description of *T. alalunga* had arisen from reliance on black pigmentation in different parts of the body. Matsumoto (1962) relied upon black pigmentation on the dorsal and ventral edges of the trunk forward of the caudal fin base, whereas Yabe and Ueyanagi (1962) relied upon black pigmentation on the tips of the upper and lower jaws and the absence of pigmentation on the trunk.

The lack of sufficient larvae fitting Matsumoto's description from areas presumed to be spawning grounds on the basis of gonad studies casts some doubt on his identification. On the other hand, good correspondence in the occurrence of larvae fitting Yabe and Ueyanagi's description with catches of adult *T. alalunga* in various areas in the Pacific seemed to support the latter identification. A study of red pigment patterns in larvae prior to preservation (Ueyanagi, 1966) reinforced Yabe and Ueyanagi's identification and description. Additional observations on red pigmentation by Matsumoto (see later discussion) confirmed Ueyanagi's results and also provided more data to enhance the reliability of red pigmentation as a supplementary character for identifying *T. alalunga*.

IDENTIFICATION OF TUNA LARVAE

With the problem of differences in the identity and description of *T. alalunga* larvae fairly well settled at the outset, there remained the tasks of evaluating the various identifying characters, not only for this species but for other tunas as well, and of describing the species at various size categories.

DEFINITION OF LARVA

In tunas, as in many other fish, it is difficult to clearly separate the larval from the juvenile stages because there is no marked metamorphosis and the usual adult characters used for species identification develop gradually and separately. It is generally accepted among workers in larval tunas that the larval stage ends when the larva has developed the full complement of spines and rays in all the fins, all the vertebrae have ossified, and the anal opening has moved back near the origin of the anal fin. For nearly all tuna species, these developments occur when the larva has attained 10 to 13 mm SL. We use this as our definition, also.

EVALUATION OF CHARACTERS

In identifying fish larvae collected in plankton nets, the easiest and perhaps the only recourse is to identify the largest stage and work down to the smallest. Unfortunately, very few tuna larvae above 9 mm SL are taken in plankton net tows so that this process cannot be followed at all times and identification, therefore, must depend upon those nonadult characters that are the most distinctive and consistent throughout the size range.

Characters that have been used in the past were reviewed and evaluated. A résumé of the usefulness of the various characters follows.

Meristic

The number of myomeres is useful in separating *Katsuwonus pelamis* (42-43) and *Euthynnus lineatus* (38-39) from other tunas, including other species of *Euthynnus*, all of which have similar numbers of myomeres (40-41). The number of fin rays and spines are not useful for separation of *Thunnus* because all species are similar in this respect.

Morphological

Shape of first dorsal fin, when completely formed, is useful to distinguish late larval stages of *K. pelamis*, *Euthynnus*, and *Auxis* from those of *Thunnus*. Preopercular spines are unreliable because they undergo rapid growth changes and position of eye relative to longitudinal axis of body needs to be determined more accurately. Distribution (number and position) of pterygiophores in the second dorsal fin in relation to neural spines is useful in separating several *Thunnus* species, but only after these bones have ossified in larvae longer than 10 mm SL. Other characters of the axial skeleton useful in identification, such as the position of the first haemal arch and the position of the zygapophyses on the vertebrae, also form late.

Measurements

Morphometrics have not been used extensively to date, although there may be some with good possibilities, such as the relations of body depth to standard length, snout length to head length, and snout length to orbit diameter. Some of the reasons for not using measurement data are that the larvae not only shrink in preservatives, but the degree of shrinkage varies in different preservatives and with duration of preservation; the distortion of the body at the time of fixing cannot be controlled; and, more important, there are too few larvae in undistorted condition for reliable measurements. Added to these are other sources of variability such as rapid changes in body parts due to growth, changes which often occur in spurts, and distension of the abdomen, as well as stretching of the body at each feeding.

Pigmentation

For the most part black pigment patterns have been the most widely used and accepted character in identifying tuna larvae. There are variations and changes in black pigment patterns on tuna larvae due to growth, but in certain areas of the body these patterns have been found to be consistent enough for identification purposes. This is particularly true of pigment patterns on the first dorsal fin, posterior half of the trunk, forebrain, and tips of both jaws. The larval size at which black pigment cells appear in certain areas of the body, especially at the upper and lower jaw tips, may be useful in separating *T. albacares* from *T. alalunga*. Red pigment patterns, although not species specific, have been useful in confirming the identification of *T. alalunga* when used in conjunction with black pigment patterns.

Of all the characters reviewed and examined, pigment patterns, both black and red, were considered to be the most reliable for identification of the larval stages, despite their known variability, when supplemented by the use of certain morphological characters such as the distribution of pterygiophores in the second dorsal fin and characteristics of the vertebral column, whenever these are developed.

VERIFICATION OF RED PIGMENTATION

Ueyanagi (1966) reported on the usefulness of red pigmentation in identifying tuna larvae. Up to then identification of tuna larvae by pigmentation had been based on black pigment only.

Ueyanagi examined 350 larvae and concluded that *T. albacares* and *T. alalunga*, which are difficult to identify by the usual diagnostic characters, could be distinguished by differences in red pigment patterns: larvae of *T. alalunga* consistently had more red pigment spots on the dorsal and ventral edges of the body and along the mid-lateral line forward of the caudal peduncle than larvae of *T. albacares;* red pigment patterns in larvae of *T. thynnus* and *T. obesus* were intermediate between those of *T. alalunga* and *T. albacares;* the red pigment pattern in *Allothunnus fallai* was similar to that in *Thunnus;* and the pattern in *K. pelamis* resembled that in *Auxis* spp. and *E. affinis* but differed from that in *Thunnus*.

To confirm these results and to provide additional information on red pigmentation in tuna larvae, the results of observations made on 432 larvae taken in Hawaiian waters during August and September 1967 were presented. Tables 1 and 2 give the number of red pigment cells along the dorsal, ventral, and lateral lines on the posterior half of the trunk and a summary of the number of larvae examined, the number of larvae observed with red pigmentation, and the mean numbers of red pigment cells at the three sites. In Table 2, the number of red pigment cells observed most frequently are given in bold face type and those observed occasionally or seldom are enclosed in parentheses.

The pigment patterns agreed generally with those reported by Ueyanagi for the species listed in the tables. Differences in the patterns were noticeable mainly in the dorsal edge of the trunk and, to a lesser extent, in the mid-lateral line. There was no significant difference in the number of pigment cells between the left and right sides of the body.

The appearance and extent of red pigment cells varied in larvae taken in night and day tows. In larvae taken at night the pigment cells were numerous, distinct, and brightly colored, whereas in larvae taken during the day the pigment cells were faintly colored, often not visible, and in many instances the pigment spots were united, forming single continuous lines. Of the species taken in both day and night tows (*T. albacares, T. obesus,* and *K. pelamis*), red pigmentation was not visible in 41.5% of the larvae taken during the day, compared with only 3.6% of the larvae taken at night. Thus, observations of red pigment cells must be made largely on larvae taken at night to reduce the effects of diel variations.

Despite the variations, red pigmentation is a useful supplementary character to either separate certain species or verify the identification made on the basis of other characters. That the red pigment pattern is not species specific is clearly seen in the similarity among *K. pelamis, Auxis* spp., and *E. affinis* and between *T. obesus* and *T. albacares*; however, it is useful in separating *T. alalunga* from the other kinds of *Thunnus*.

EXAMINATION AND DISCUSSION OF SPECIES

Thunnus alalunga and *T. albacares*

Larvae of these two species were examined together because they are the only species lacking black pigment cells on the trunk, exclusive of the caudal fin and abdomen (Yabe and Ueyanagi, 1962). Characters, including some that have not been used in the past, for separating the two species are summarized in Table 3. The larval stage was divided into two size categories, small larvae less than 10 mm SL and larger larvae 10 to 13 mm SL, because the characters used in differentiating small larvae became ineffective or obscured with growth. As mentioned earlier, pigmentation, particularly the presence of black pigment cells at the tips of the upper and lower jaws and the amount of red pigment cells on the trunk, was the most reliable character in separating larvae of the two species.

In small larvae, black pigment cells on the lower jaw tip were first observed in larvae of *T. albacares* about 4.5 to 6.0 mm SL, and often as small as 3.8 mm SL; those on the upper jaw tip were first observed in larvae about 7.0 mm SL (Figures 1 and 2, reproduced from Matsumoto, 1958[7]). In *T. alalunga* these pigment cells were

[7] The difference in developmental stages per given size in the figures by Matsumoto (1958) and Ueyanagi (1969) is due to method of preservation: Matsumoto's figures are of larvae preserved in 10% Formalin; Ueyanagi's figures are of larvae preserved in 70% alcohol.

TABLE 1.—Frequency of red pigment cells in larval tunas from Hawaiian waters, August-September 1967.

Part of body	No. of pigment cells	*Thunnus albacares*			*Thunnus obesus*			*Thunnus alalunga*			*Katsuwonus pelamis*			*Auxis* spp.			*Euthynnus affinis*		
		Left side	Right side	Percent occurrence[1]	Left side	Right side	Percent occurrence[1]	Left side	Right side	Percent occurrence[1]	Left side	Right side	Percent occurrence[1]	Left side	Right side	Percent occurrence[1]	Left side	Right side	Percent occurrence[1]
Dorsal edge trunk	0	56	52	51.9	26	26	57.7	---	---	---	86	87	99.4	49	20	94.5	8	7	100.0
	1	42	32	35.6	16	18	37.7	---	---	---	---	---	---	2	2	5.5	---	---	---
	2	10	9	9.1	4	---	4.4	3	3	46.1	1	1	0.6	---	---	---	---	---	---
	3	4	2	2.9	---	---	---	3	3	46.1	---	---	---	---	---	---	---	---	---
	4	---	1	0.5	---	---	---	1	---	7.7	---	---	---	---	---	---	---	---	---
Total		112	96	---	46	44	---	7	6	---	87	88	---	51	22	---	8	7	---
Mid-lateral line trunk	0	4	9	6.3	11	8	21.6	---	---	---	85	86	97.7	35	16	70.0	6	7	86.7
	1	12	11	11.2	6	8	15.9	---	---	---	1	---	0.6	13	5	24.6	---	---	---
	2	45	34	38.3	11	13	27.3	---	1	7.7	1	1	1.1	2	1	4.1	1	---	6.7
	3	31	24	26.7	10	8	20.4	3	2	38.4	---	1	0.6	1	---	1.4	1	---	6.7
	4	14	14	13.6	7	5	13.6	3	3	46.1	---	---	---	---	---	---	---	---	---
	5	4	3	3.4	---	1	1.1	1	---	7.7	---	---	---	---	---	---	---	---	---
	6	1	---	0.5	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Total		111	95	---	45	43	---	7	6	---	87	88	---	51	22	---	8	7	---
Ventral edge trunk	0	1	---	0.5	---	1	1.2	---	---	---	1	---	0.6	---	---	---	---	---	---
	1	---	---	---	2	---	2.4	---	---	---	2	2	2.3	---	---	---	---	---	---
	2	1	---	0.5	1	---	1.2	---	---	---	3	5	4.6	4	2	8.2	---	---	---
	3	2	7	4.6	3	4	8.6	---	---	---	5	5	5.7	4	---	5.5	---	---	---
	4	6	9	7.7	7	5	14.8	---	---	---	6	4	5.7	3	1	5.5	---	1	6.7
	5	13	16	14.9	12	10	27.1	1	---	7.7	9	12	12.0	2	5	9.6	1	3	26.7
	6	19	14	17.0	8	10	22.1	2	---	15.4	8	8	9.0	3	1	5.5	3	---	20.0
	7	22	14	18.5	5	4	11.1	1	3	30.8	17	8	14.3	5	2	9.6	---	1	6.7
	8	14	12	13.4	4	3	8.6	2	---	15.4	7	12	10.8	10	3	17.8	1	2	20.0
	9	6	7	6.7	---	1	1.2	---	1	7.7	12	10	12.6	3	1	5.5	2	---	13.3
	10	7	5	6.2	---	---	---	---	1	7.7	6	10	9.1	8	4	16.4	1	---	6.7
	11	3	2	2.6	---	---	---	---	---	---	6	5	6.3	1	1	2.7	---	---	---
	12	3	1	2.1	---	1	1.2	1	1	15.4	1	4	3.9	6	1	9.6	---	---	---
	13	1	---	0.5	---	---	---	---	---	---	---	1	0.6	---	1	1.4	---	---	---
	14	2	1	1.5	---	---	---	---	---	---	---	1	1.7	2	---	2.7	---	---	---
	15	---	2	1.0	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
	16	1	---	0.5	---	---	---	---	---	---	1	1	1.1	---	---	---	---	---	---
	17	---	---	---	---	---	---	---	---	---	1	---	0.6	---	---	---	---	---	---
	18	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
	19	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
	20	1	1	1.0	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Total		103	91	---	42	39	---	7	6	---	87	88	---	51	22	---	8	7	---

[1] Percent occurrence refers to left and right sides combined.

TABLE 2.—Summary of red pigment cells in larval tunas from Hawaiian waters, August-September 1967.

Species	Number larvae examined	Larvae with red pigment	Red pigment cells on posterior half of trunk					
			Dorsal edge		Mid-lateral line		Ventral edge	
			Number[1]	Mean	Number[1]	Mean	Number[1]	Mean
Thunnus albacares	130	112	**0**, 1, 2, (3)	0.6	(0), 1, **2**, 3, **4**, (5)	2.4	3-12	7.0
Thunnus obesus	63	47	**0**, 1, (2)	0.5	0, 1, **2**, 3, 4	1.9	1-8	5.3
Thunnus alalunga	6	6	**2, 3,** (4)	2.6	(2), 3, **4**, (5)	3.5	5-12	8.0
Katsuwonus pelamis	138	88	**0**	0.0	**0**	0.0	1-12	7.2
Auxis spp.	72	51	**0**, (1)	0.0	**0**, 1, (2)	0.4	2-14	7.6
Euthynnus affinis	23	8	**0**	0.0	**0**, (2), (3)	0.3	4-10	6.7
Total	432	312						

[1] Less than 2% occurrence omitted.

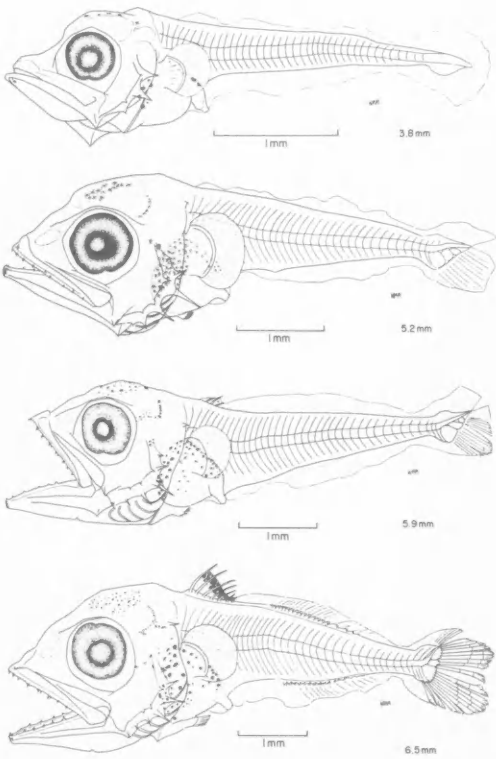

FIGURE 1.—Larval stages of *Thunnus albacares*, I. (From Matsumoto, 1958. Lengths have been converted from total to standard.)

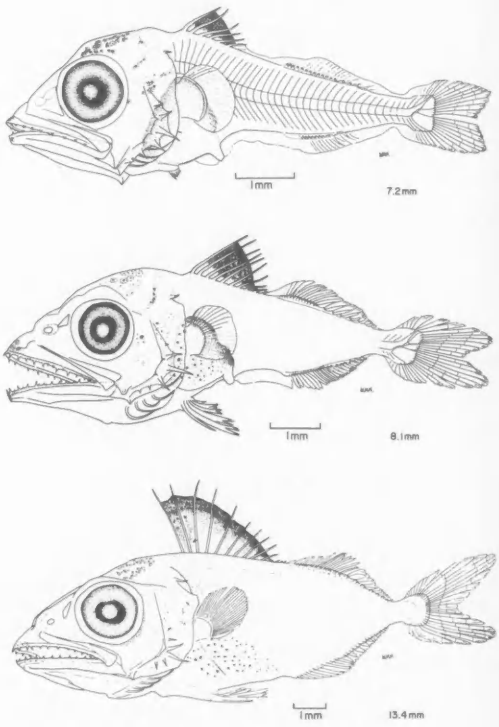

FIGURE 2.—Larval stages of *Thunnus albacares*, II. (From Matsumoto, 1958. Lengths have been converted from total to standard.)

first observed on the upper jaw tip in larvae about 5.0 mm SL and on the lower jaw tip at about 9.0 to 10.0 mm SL (Figures 3 and 4, reproduced from Ueyanagi, 1969). Consequently, all larvae between 4.5 and 7.0 mm SL having black pigment cells only on the lower jaw tip, and larvae between 7.0 and 9.0 mm SL having black pigment cells on the tips of both jaws were considered as *T. albacares*. All larvae between 5.0 and 9.0 mm SL having black pigment cells

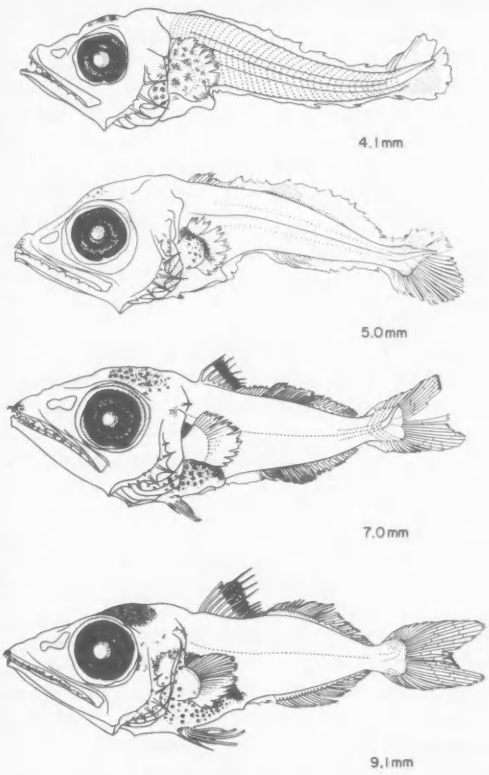

FIGURE 3.—Larval stages of *Thunnus alalunga*, I. (From Ueyanagi, 1969. Lengths have been converted from total to standard.)

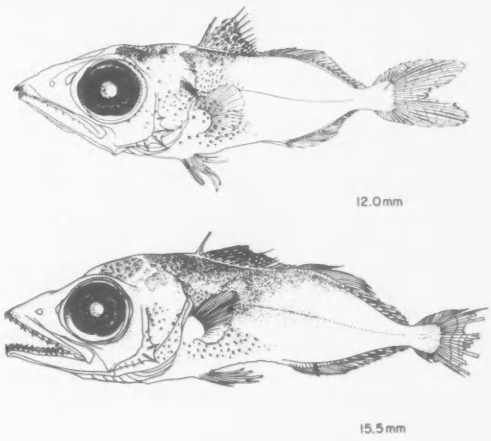

FIGURE 4.—Larval stages of *Thunnus alalunga*, II. (From Ueyanagi, 1969. Lengths have been converted from total to standard.)

only on the upper jaw tip were considered as *T. alalunga*. Larvae of the two species from 9.0 to 10.8 mm SL were separated by the position of black pigment cells on the lower jaw tip: in *T. albacares* the pigment cells were located on the inner, and sometimes outer, margins in larvae up to 10.8 mm SL, but in *T. alalunga* they were found only on the outer margin. It is suspected that the black pigment cells on the inner margin of the jaw in *T. albacares* migrate to the outer margin with further growth of the larvae.

Red pigmentation was accepted as a good supplementary character for separating *T. albacares* from *T. alalunga* (Tables 1 and 2). The distinctive patterns were located along the dorsal margin of the trunk from about the midpoint of the second dorsal fin base to the caudal peduncle. In *T. albacares* there was usually none or one red pigment cell at the caudal peduncle. Two pigment cells occurred seldom and three or four pigment cells occurred only rarely. Generally, these pigment cells were clustered at the caudal peduncle region. In *T. alalunga* there were usually two or three pigment cells, sometimes as many as four. Unlike those in *T. albacares*, these pigment cells were well spaced, extending forward to the middle of the second dorsal fin base. Only minor differences were noted in the red pigment cells along the mid-lateral line.

In larger larvae (10-13 mm SL) differences in the two species were noted in the distribution of pterygiophores of the second dorsal fin on cleared and stained specimens (Table 3). In *T. albacares* the two successive single pterygiophores between two adjoining neural spines occurred at the posterior end, whereas in *T. alalunga* they were at the anterior end. Additionally, the first haemal arch was on the 11th vertebra in *T. albacares* and on the 10th vertebra in *T. alalunga*.

TABLE 3.—Characters to separate larvae of *Thunnus albacares* and *Thunnus alalunga*.

Characters	*T. albacares*	*T. alalunga*
Small larvae (4-10 mm SL):		
Black pigmentation:		
Upper jaw	Appears at about 5.8 mm SL, mostly after 6.0 mm SL	Appears at about 5.0 mm SL
Lower jaw	Appears at 4.5-6.0 mm SL	Appears at 9-10 mm SL
	At tip on inner edge; migrate to outer edge with further growth	At tip on outer edge
Red pigmentation:		
Dorsal edge body, postanus	**0**, 1, 2, (3) [mean = 0.6]; near caudal peduncle	**2**, **3**, (4) [mean = 2.6] from peduncle to mid-second dorsal fin base
Lateral line, postanus	(0), 1, **2**, 3, 4, (5) [mean = 2.4]	(2), **3**, **4**, (5) [mean = 3.5]
Ventral edge body, postanus	3-12 [mean = 7.0]	5-12 [mean = 8.0]
Large larvae (>10 mm SL):		
Array of [1]D_2 pterygiophores between two adjacent neural spines	1, 2, 2, 2, 3, 2, 1, 1	1, 1, 2, 2, 2, 3, 2, 1
Position of first haemal arch (vertebra number)	11th	10th

[1] D_2 refers to second dorsal fin.

Other *Thunnus* species

These species, which include *T. thynnus* (*T. thynnus thynnus* of Atlantic and *T. thynnus orientalis* of Pacific), *T. tonggol*, *T. maccoyii*, and *T. obesus*, have been identified mainly by black pigmentation on the trunk other than that over the abdominal wall.

In small *T. thynnus* of both Atlantic and Pacific Oceans (larvae between 3 and 10 mm SL), one or two large black pigment cells are present on the dorsal edge of the trunk between the second dorsal and caudal fins (Table 4, Figures 5 and 6), the anterior one usually being the larger. There may also be one to four black pigment cells on the ventral edge of the trunk between the anus and the caudal fin. Black pigmentation in *T. thynnus* from both oceans agrees quite well, except that in 5 out of 10 Atlantic specimens one or two tiny black pigment cells were noted along the mid-lateral line of the body near the pectoral fin, and in two instances a single tiny black pigment cell was found on the mid-lateral line beneath the posterior end of the second dorsal fin. These pigment cells were not considered reliable for identification purposes.

Observation of red pigmentation on larvae of Atlantic and Pacific *T. thynnus* is incomplete. Only one Atlantic *T. thynnus* larvae was examined for this character, but unfortunately the specimen was taken in a day tow so that the pigmentation appeared as a continuous streak on both the dorsal and ventral edges of the trunk as well as on the ventral surface of the lower jaw. In Pacific *T. thynnus* there were one to five red pigment cells, usually three, on the dorsal edge of the trunk. The number of red pigment cells on the mid-lateral line and ventral edge of the trunk has not been recorded, but according to the illustration by Ueyanagi (1966), the pigment pattern may be similar to that of *T. obesus*. On the basis of black and red pigmentation, the Atlantic and Pacific *T. thynnus* were not separable.

The identification of *T. tonggol*, based on size series of 4.2 to 7.3 mm, has yet to be confirmed. Following the description of the species by Matsumoto (1962), larvae similar to these having the anteriormost black pigment cell on the dorsal edge of the body ahead of the second dorsal fin origin have been found in 1963 in the mid-South Atlantic Ocean near Ascension Island. Confirmation of the species description requires the finding of adults within this area and the finding of additional larvae to extend the identified size range.

The identification of *T. maccoyii*, which was first described as having black pigment pattern similar to that of *T. thynnus* (Yabe, Ueyanagi, and Watanabe, 1966) and later as having the black pigment cells on the dorsal edge of the trunk reduced to pinpoints (Ueyanagi, 1969), also needs verification (see discussion on *T. thynnus*). The correspondence of published descriptions based on eight specimens and observations of larvae identified as this species were not conclusive.

T. obesus was easily separated from *T. thynnus* by the absence of black pigmentation on the bases of the anterior dorsal finlets. Sometimes a single small black pigment cell was present along the ventral edge of the trunk near the caudal peduncle, but more often one to three pig-

TABLE 4.—Characters used to separate larvae of *Thunnus* species having black pigmentation on trunk.

Characters	*Thunnus thynnus* (Atlantic)	*Thunnus thynnus* (Pacific)	*Thunnus tonggol*	*Thunnus maccoyii*	*Thunnus obesus*
Small larvae (3-10 mm SL):					
Number of black pigment cells:					
Upper jaw tip	No observation	Appears above 6 mm SL	No observation	Appears above 5 mm SL	Few spots above 5 mm SL
Lower jaw tip	2 on inner edge	2 on inner edge above 4 mm SL	No observation	Appears above 4 mm SL	0-2 on inner edge below 4 mm SL
Dorsal edge trunk	1 or 2	1 or 2	1, 2, or more	1 or 2, very small	None
Lateral line	0-2 near mid-trunk	None	None	0 or 1 near mid-trunk	None
Ventral edge trunk	1-4	2 or more	2 or more	1-3	1 or more
Number of red pigment cells:					
Dorsal edge trunk	Streak on caudal peduncle[1]	1-5, mostly 3	No observation	No observation	0, 1, (2)
Lateral line	Indistinct[1]	Number not available	No observation	No observation	0, 1, 2, 3, 4
Ventral edge trunk	Streak anus to caudal peduncle[1]	Number not available	No observation	No observation	1-8 [mean = 5.3]
Lower jaw ventral view	Streak along margin anterior half of jaw and midline[1]	2 well spaced on anterior half	No observation	No observation	1 on each side near tip
Large larvae (>10 mm SL):					
Array of [2]D_2 pterygiophores between two adjacent neural spines	1, 2, 2, 3, 2, 2, 1, 1	No observation	No observation	No observation	1, 2, 2, 2, 3, 2, 1, 1

[1] Only one larva taken in a day tow was examined.
[2] D_2 refers to second dorsal fin.

ment cells were present along the base of the posterior half of the anal fin. Red pigmentation did not differ from that in *T. albacares*.

In larger larvae (10-13 mm SL) the array of pterygiophores of the second dorsal fin between two adjacent neural spines was sufficient to separate *T. thynnus* from *T. obesus* and both species from *T. alalunga* (Tables 2 and 3). In *T. thynnus* the greatest number of pterygiophores (3) between two adjacent neural spines appeared in the fourth position in the array, whereas in *T. obesus* and *T. alalunga* it appeared in the fifth and sixth positions, respectively. *T. obesus* was not distinguishable from *T. albacares* by this character.

The identification of *T. atlanticus* was not resolved. No larvae from the distributional range of this species (tropical western Atlantic) have been found which are distinguishable from any of the species considered above. One of us (Richards) suspects that *T. atlanticus* larvae are very similar to larvae of *T. obesus*. This suspicion is based on the great abundance of larvae resembling those of *T. obesus* in this area, particularly at times and places where *T. obesus* adults are rarely found or absent. Further studies are needed.

SUMMARY OF LARVAL IDENTIFICATION

On the basis of the examination and discussion above, the workshop agreed that:

1. The description of *T. albacares* by Matsumoto (1958) was correct (see Figures 1 and 2), but that the "appearance of black pigmentation at the tip of the lower jaw at about 4.5 mm SL" should be included.

2. The description of *T. alalunga* by Yabe and Ueyanagi (1962) and illustrations by Ueyanagi (1969) were correct (see Figures 3 and 4), but that the lower size limit should be set at about 4.5 mm SL until further studies indicate more precisely the earlier appearance of black pigmentation at the tip of the lower jaw in *T. albacares*.

3. It is not possible to separate larvae of *T. albacares* from *T. alalunga* below 4.5 mm SL, prior to the appearance of black pigment cells at the tip of the lower jaw in *T. albacares*.

4. The description of *T. thynnus* by Yabe, Ueyanagi, and Watanabe (1966) was correct

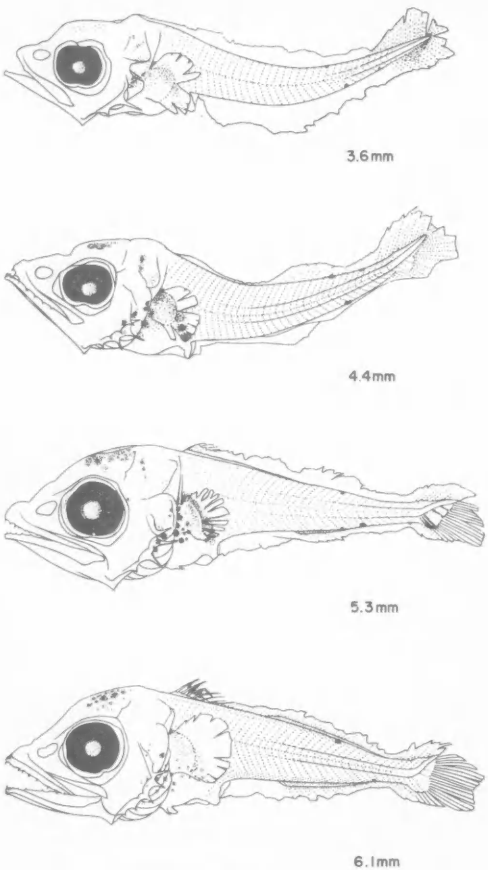

FIGURE 5.—Larval stages of *Thunnus thynnus*, I. (From Yabe, Ueyanagi, and Watanabe, 1966. Lengths have been converted from total to standard.)

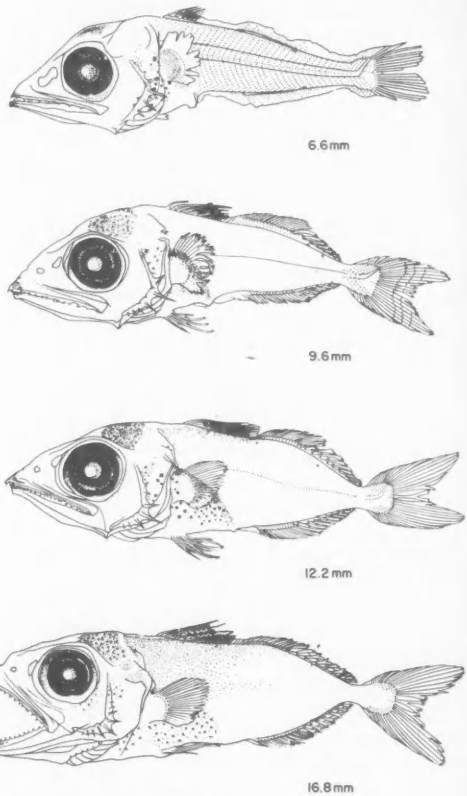

FIGURE 6.—Larval stages of *Thunnus thynnus*, II. (From Yabe, Ueyanagi, and Watanabe, 1966. Lengths have been converted from total to standard.)

(see Figures 5 and 6), and that there was no difference in *T. thynnus* from the Atlantic and Pacific Oceans.

5. The identification of *T. tonggol* was not substantiated by an adequate size series.

6. The description of *T. maccoyii*, based on tiny melanophores on the dorsal edge of the trunk, was not conclusive.

7. The description of *T. obesus* by Matsumoto (1962) was correct, though it needed to be augmented by illustrations of a complete size series.

8. The identity of *T. atlanticus* larvae is unresolved.

IDENTIFICATION OF JUVENILES

In spite of the intention of the workshop to assemble as many specimens of juvenile tunas as possible, only a few juveniles of *T. albacares* and *T. obesus*, not nearly enough to warrant their detailed examination, were available for study. The discussion on juvenile tuna identification, therefore, dealt mainly with published reports and with contributed data, resulting in a summary of identifying characters which the workshop considered useful and reliable.

Once the young tuna has acquired the full complement of spines and rays in all the fins, complete ossification of all the vertebrae, and the relocation of the anus near the origin of the anal fin, it is generally considered a juvenile of the species. Certain characters such as the full number of gill rakers, however, develop much later, when the juvenile has attained a length of 40 or 45 mm SL. If we consider juveniles to include all sizes up to the time of full gonad development signified by initial spawning, the size range of the juvenile stage would extend from about 13 mm SL to 700 mm FL (fork length) in *T. albacares* (Yuen and June, 1957) and to 860 mm FL in *T. alalunga* (Otsu and Hansen, 1962). For the purpose of clarifying species identification of the young, however, individuals beyond 200 mm SL need not be included. The term juvenile, as used here, thus refers to tunas between 13 and 200 mm SL.

EVALUATION OF CHARACTERS

The greatest difficulty in identifying juveniles of *Thunnus* is that the most useful characters are located internally. Except for the flattened first elongate haemal spine in *T. alalunga*, there is no single character that is peculiar to each of the species; but by using a combination of characters it should be possible to identify most of the other species. A summary of the most useful characters discussed is listed in Table 5. The size of juvenile at which each of the characters can be observed is listed also. Those characters whose usefulness in the early juvenile stages has not been shown conclusively are indicated by a question mark (?). The general formula of distribution of pterygiophores of the second dorsal fin has not been used before.

The counts and descriptions given for those characters listed with a question mark generally are those of the adults. These have not yet been substantiated for juveniles as well. Changes in the position of the first haemal arch with growth, for example, have been known to exist in other closely related fish such as the wahoo, *Acanthocybium solandri* (Matsumoto, 1967). This could be true of the tunas also.

Comparisons of body parts, particularly of orbit diameter, body depth at origins of the first dorsal and anal fins, preanal and postanal distances, and snout length, have not been investigated sufficiently in the past. The unavailability of specimens in sufficient numbers as well as the nonuniformity of body lengths (fork and standard) used have contributed greatly to this neglect. Acceptance of standard length as the standard measure of body length and publishing of actual measurements in the future should help in the accumulation of sufficient data for analyses. This has to be done by all workers in this field of study, since the juveniles are not easily taken in large numbers.

TABLE 5.—Characters for separating juveniles of *Thunnus* species.

Character	Useful on juveniles above	*Thunnus thynnus*	*Thunnus alalunga*	*Thunnus atlanticus*	*Thunnus obesus*	*Thunnus albacares*
First haemal arch	?	10	10	11	11	11
Ceratobranchial including angle	40 mm SL	17-20	15-16	12-13	15-16	15-16
Vertebrae	13 mm SL	18 + 21	18 + 21	19 + 20	18 + 21	18 + 21
Array of $^{1}D_2$ pterygiophores between two adjacent neural spines	10 mm SL	1, 2, 2, 3, 2, 2, 1, 1	1, 1, 2, 2, 2, 3, 2, 1	1, 2, 2, 2, 3, 2, 1, 1	1, 2, 2, 2, 3, 2, 1, 1	1, 2, 2, 2, 3, 2, 1, 1
First prezygapophysis and position on haemal arch	?	15, 16, 17, high	15, 16, high	16, 17, low	15, 16, high	13, 14, low
Postzygapophysis near first prezygapophysis	?	Short, directed posterior	Short, directed posterior	Long, directed vertical or slightly anterior	Short, directed posterior	Long, directed vertical, some slightly anterior
First haemal spine	30 mm SL	Winglike at some stages	Extremely winglike	Winglike at some stages	--	--
Lateral line above base of pectoral fin	25 mm SL	Acute, nearly 90°	Obtuse	Obtuse	Obtuse	Obtuse

[1] D_2 refers to second dorsal fin.

DISCUSSION AND SUMMARY

T. thynnus below 25 mm SL can be separated from the other *Thunnus* species by the array of pterygiophores of the second dorsal fin, the last four positions containing 2, 2, 1, 1 pterygiophores; in *T. alalunga* the sequence is 2, 3, 2, 1, and in *T. atlanticus*, *T. obesus*, and *T. albacares* it is 3, 2, 1, 1. *T. thynnus* above 25 mm SL can be separated from all other *Thunnus* by the sharp angle (nearly 90°) which the lateral line follows near the base of the pectoral fin; in all other species this angle is obtuse. In juveniles above 40 to 45 mm SL, *T. thynnus* has the highest number of gill rakers on the ceratobranchial, including that at the angle (Potthoff and Richards, 1970).

T. alalunga below 30 mm SL can be separated from other *Thunnus* species by the distribution of pterygiophores of the second dorsal fin. Above 30 mm SL, *T. alalunga* is the only species whose first elongated haemal spine is flattened laterally and appears extremely winglike.

T. atlanticus as small as 13 mm SL can be separated from other *Thunnus* species by its distinctive precaudal and caudal vertebral counts. It is the only species having 19 precaudal and 20 caudal vertebrae. Above 40 to 45 mm SL, this species can be separated from the others by the low (12-13) gill raker count on the ceratobranchial (Potthoff and Richards, 1970), in addition to the vertebral formula.

T. obesus and *T. albacares* are the only two species that cannot be distinguished from each other on the basis of internal characters. Comparisons of body parts, i.e., orbit diameter, body depth or preanal and postanal distances, may have to be used.

ACKNOWLEDGMENTS

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THE FERTILIZATION OF GREAT CENTRAL LAKE. I. EFFECT OF PRIMARY PRODUCTION

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ABSTRACT

Commercial fertilizer was added at a rate of 5 tons per week to a lake (51 km^2, mean depth 200 m) over a period of 5 months from May to October 1970. As a result of these additions, surface primary production was increased approximately tenfold while the primary production of the euphotic zone was doubled. The standing stock of primary producers and water clarity were substantially the same as in the previous year when no fertilizer was added. The productive index (mg C/mg Chl *a*/hr) was increased, especially in the immediate area of nutrient enrichment. However, the principal phytoplankton species were very similar at locations near and distant from the area of fertilization. In conclusion, it appears that as a result of adding nutrients at a low but sustained level, primary productivity was increased without substantially changing the nature of the food chain at the primary level of production.

In the Pacific northwest, an earlier study (Nelson and Edmondson, 1955) on the fertilization of a small salmon-producing lake in Alaska showed that the addition of phosphate and nitrate fertilizer increased the production of sockeye salmon (*Oncorhynchus nerka*); in more recent studies by Donaldson et al. (1968), an increase in the production of steelhead trout (*Salmo gairdneri*) was demonstrated in a small lake in the state of Washington. The natural fertilization of lakes from decomposing salmon carcasses has been discussed by Krokhin (1967), who has suggested that the potential deficit from salmon removed by the fishery should be replaced by artificial fertilization. In the report presented here we have carried out a fertilization experiment which differs from the two previous reports (Nelson and Edmondson, 1955; Donaldson et al., 1968) in several respects. These include the size scale of the experiment which was very much larger than any previous experiments, the application of fertilizer as a solution, control of the N:P ratio, and, finally, sustained weekly nutrient additions over a period of 5 months.

Preliminary results of our experiment have been reported (Parsons et al., in press) together with our conclusion that lake production was increased by the addition of fertilizer and that this was achieved without causing a condition of eutrophication. The following account deals specifically with the effect of nutrient enrichment on the primary level of production. Intensive studies on the effect of nutrient additions were carried out during the period May to August 1970 while a more general monitor program has been maintained from 1969 to the present (March 1971). The first sustained nutrient additions were made during the period June to October 1970 and further additions are planned for the next 5 years.

The primary purpose in this study is to increase levels of production in an oligotrophic lake, but not to change the trophic relationships which lead to the production of young sockeye salmon. In this respect the ultimate desideratum of the experiment is to produce larger sockeye smolts at their time of seaward migration; earlier reports have demonstrated that there is a close positive relationship between smolt size and survival (Ruggles, 1965; Johnson, 1965). Since previous studies (Parsons et al., in press) have shown that the migrant smolts from Great Central Lake are small (63 ± 1 mm) and that the primary productivity is very low (ca. 5 g

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C/m²/year), application of nutrients at a level that would increase primary and secondary production seemed reasonable.

Data used in this presentation have been obtained from Stephens et al. (1969[3]) and Kennedy et al. (1971[4]).

METHODS

ANALYTICAL PROCEDURES

Chlorophyll *a*, nutrients, oxygen, and total CO_2 were all measured as described previously (Strickland and Parsons, 1968); bacteria were enumerated from plate counts after 24 hr incubation at room temperature on Millipore universal medium; major phytoplankton species were enumerated after settling preserved samples; conductivity was measured using a Beckman Solu Bridge (Cedar Grove, N.J.). Primary productivity was measured as the difference in uptake of $^{14}CO_2$ in light and dark bottles; however, on a few days the dark-bottle uptake was exceptionally high and this requires further investigation. For the purpose of this presentation, data have been used only for days when the dark-bottle uptake was less than 20% of the maximum light-bottle uptake.

Radiation was measured with an Epply pyranometer and corrected to give photosynthetically available radiation (PAR) as described previously (Parsons and Anderson, 1970). Light attenuation was routinely measured with a Secchi disc (SD), and an empirical relationship between SD depth (m) and the vertical extinction coefficient was established using a Schüler meter (maximum response at 430 nm). This relationship for light at 430 nm was:

$$K_{10}^{430} = \frac{2.1}{\text{SD depth}}$$

The (total) extinction coefficient for the water column was then found from Jerlov's (1957) light attenuation curves. Mean radiation (I_m) for the water column of depth (d_m) was determined from the expression

$$I_m = \frac{I_0\,(1-e^{-kd_m})}{d_m k}$$

where I_0 was the surface radiation and k was the attenuation coefficient for light below the surface meter. The expression was also used to determine the light at various depths in relation to the photosynthetic activity at those depths.

NUTRIENT ADDITIONS

The choice of a suitable fertilizer for the waters of Great Central Lake has been discussed previously (Parsons et al., in press). The nutrient addition consisted of a commercial grade of ammonium phosphate and ammonium nitrate which contained trace quantities of other elements essential for plant growth. The mixture is known commercially as 27-14-0 (27% N; 14% P_2O_5; 0% K_2O) and has an N:P ratio of 10:1.

The ammonium nitrate and ammonium phosphate were dissolved separately in 5-ton amounts (total) and the concentrated solutions mixed before distribution. A small quantity of organic material was added to the dissolved inorganic fertilizer at a dilution of 6 liters of fish solubles (obtained from B.C. Packers Ltd.) for every 2 tons of nutrient solution. The dissolved fertilizer was distributed at 10 gal/min (38 liters/min) in the wake of a vessel travelling at approximately 8 knots. The area of nutrient additions is shown in Figure 1, together with sampling stations 1, 2, and 3. Station 1 was sampled during 1969 and 1970, Station 2 was sampled during 1970, and Station 3 was sampled sporadically during 1970 in order to check on the flow of nutrients in a westerly direction; in addition, areal surveys for chlorophyll *a*, transparency, and bacteria were carried out over the whole lake in order to determine within-lake variation.

The area over which nutrients were added represented ca. 3 sq mi (8 km²) of lake surface; however, from studies on lake circulation it was apparent that the material was transported east

[3] Stephens, K., R. Neuman, and S. Sheehan. 1969. Chemical and physical limnological observations, Babine Lake, British Columbia, 1963 and 1969, and Great Central Lake, British Columbia, 1969. Fish. Res. Board Can., Manuscr. Rep. 1065: 41-52.

[4] Kennedy, O. D., K. Stephens, R. J. LeBrasseur, T. R. Parsons, and M. Takahashi. 1971. Primary and secondary production data for Great Central Lake, B.C., 1970. Fish. Res. Board Can., Manuscr. Rep. 1127. 379p.

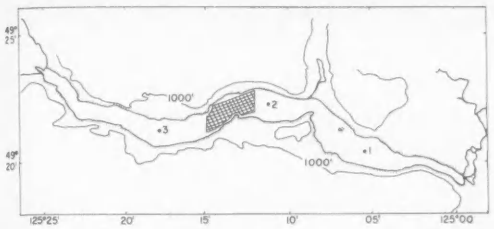

FIGURE 1.—Great Central Lake showing principal sampling stations (1, 2, and 3) and area of nutrient enrichment (crosshatched).

and west at rates of up to 6 miles per day or ca. 10 km/day (Parsons et al., in press). Thus while Station 2 was generally under the most immediate influence of the nutrient additions, Stations 1 and 3 also received an accumulative enrichment. Fertilizer was added at the rate of 5 tons per week from June through to October 1970. During May 1970 approximately 2 tons of fertilizer were added in experiments to determine the rate of mixing and distribution of nutrients in the vessel's wake.

RESULTS

LAKE MORPHOMETRY

Great Central Lake is located on Vancouver Island, B.C., at lat 49°20′ N on an east/west axis between long 125°00′ W and 125°25′ W (Figure 1). It is a long narrow lake (ca. 33 × 1.5 km) with steep sides and a mean depth of 200 m. The yearly mean discharge is approximately 6 × 10^6m^3/day with a range from 0.4 × 10^6 to 32 × 10^6m^3/day.

TEMPERATURE

The temperature structure at Station 1 is shown in Figure 2. The results are representative for the open waters of the whole lake, and it is apparent that the lake was isothermal during January and February; a thermocline started to form during March and was well established by May. Maximum surface temperature during July was 21.2° C; surface cooling started in September but a thermocline of

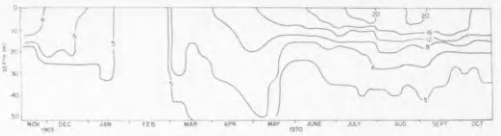

FIGURE 2.—Temperature (°C) stratification at Station 1.

10° persisted through October and the lake did not become isothermal until January of the following year.

RADIATION

Changes in photosynthetically active radiation (PAR) at the lake surface are shown in Figure 3 together with the mean radiation for the water column 0 to 20 m, calculated on a 24-hr basis.

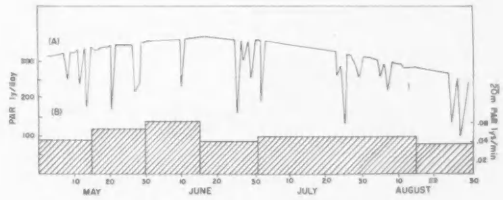

FIGURE 3.—(A) Surface photosynthetically active radiation (PAR) and (B) 15-day mean PAR in the first 20 m.

From the latter results it is apparent that radiation in the water column increased by 50% from the beginning of May until the middle of June; the decrease in radiation during the second part of June was due to a combination of higher extinction coefficients and lower surface radiation. The average radiation remained virtually constant during July and decreased by 20% during the latter half of August.

CHLOROPHYLL *A*

Surface chlorophyll *a* concentrations are presented in Figure 5 in the same way and for the same stations and years as SD data in Figure 4. The two figures have some mirrored similarities;

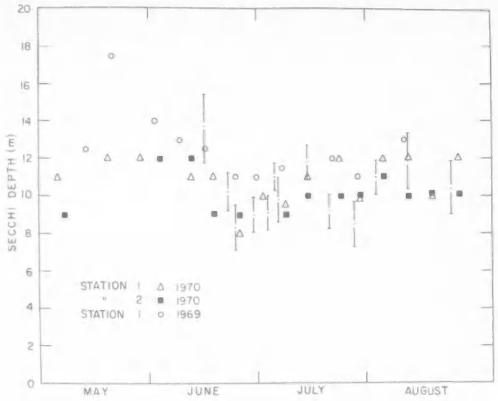

FIGURE 4.—Secchi disc depth at Stations 1 and 2, 1970, and Station 1, 1969. (Mean and standard deviation of values from areal surveys shown as bars.)

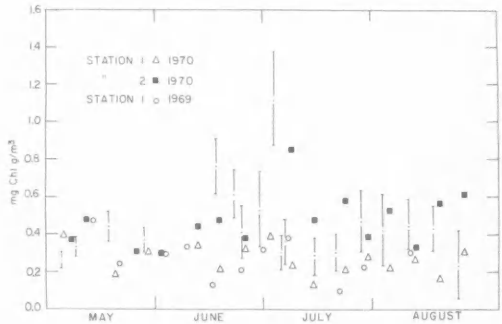

FIGURE 5.—Surface chlorophyll *a* data at Stations 1 and 2, 1970, and Station 1, 1969. (Mean and standard deviation of values from areal surveys shown as bars.)

thus Station 2 chlorophyll *a* values from June to August were generally higher than either Station 1 data for 1969 or 1970; minimum mean SD data (8 to 10 m) occurred between June and July during a maximum in the mean chlorophyll *a* concentration. However, 1969 chlorophyll *a* data at Station 1 do not appear to be significantly different from 1970 chlorophyll *a* data at the same station.

The depth distribution of chlorophyll *a* generally showed a maximum between 10 and 20 m following stratification and nutrient depletion in the surface layers.

pH, CALCIUM, TOTAL CO_2, AND CONDUCTIVITY

pH values were generally between 7.1 and 8.3 with some indication of a seasonal cycle towards higher pH values in summer. Several assays for calcium showed a concentration of 5 mg/liter while specific conductivity was very consistent at 33 μ mhos/cm, except in the immediate vicinity of small streams entering the lake; total carbon dioxide varied over a range from about 2.2 to 4.2 mg C/liter.

OXYGEN

Oxygen profiles to 200 m showed that surface oxygen concentrations were between 80 and 90% saturation during winter and up to 110% saturation during summer. Deepwater oxygen concentrations appeared constant at around 10 mg/liter or about 80% saturation. An oxygen maximum occurred at ca. 20 m during the summer.

NITRATE, AMMONIA, PHOSPHATE, AND SILICATE

Nitrate depth profiles at Station 1 during May to October, 1969 and 1970, are shown in Figure 6. The general form of the two profiles is similar; thus a depletion in the winter level of nitrate (1.0 to 2.0 μg at./liter) becomes apparent towards the end of May and by the end of June about 1 μg at. NO_3N/liter has been removed from the water column, 0 to 10 m. During July and August nitrate in the first 10 to 15 m is close to the limit of detection, but there is a partial return to winter levels during September and October. Some difference in the form of these events is apparent between 1969 and 1970; the utilization of nitrate was more rapid and apparently more complete during 1970; in addition, surface nitrates did not increase in September-October 1970 as they did in 1969.

Starting from a winter level of 2 μg at. NO_3-N/liter, the total utilization of nitrate in the water column has been determined for the periods February to May, June, and July-August using data shown in Figure 7. The accumulative amount

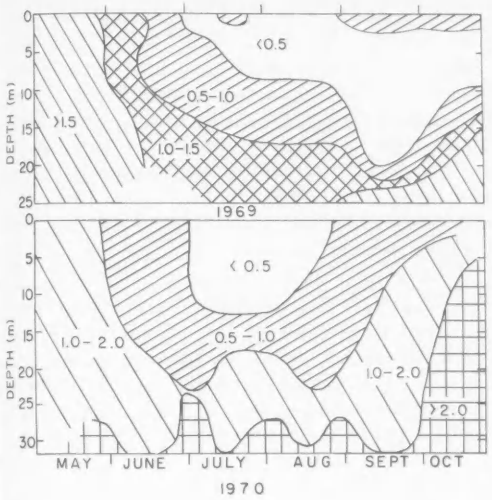

FIGURE 6.—Nitrate (μg at./liter) profiles at Station 1, May to October 1969 and 1970.

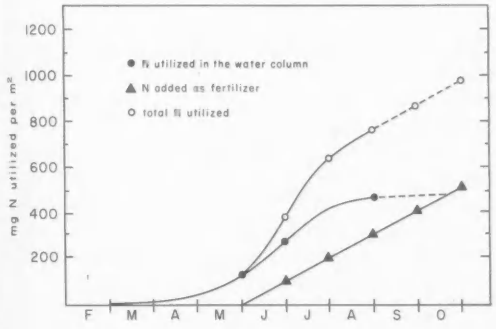

FIGURE 7.—N utilization at Station 1.

of inorganic nitrogen added as fertilizer (expressed per m^2 for the entire 51 km^2 lake surface) is also shown; since this was utilized within hours following each addition, the total nitrogen budget is represented as the sum of the natural and added inorganic nitrogen. Some mixing occurred during September and October, and the utilization of inorganic N during this period is shown as an indefinite extrapolation of the nitrogen utilized by the end of August. From these curves and Figure 5 it may be seen that the fertilizer was the principal source of new nitrogen during the period July-August when the lake nitrate was practically exhausted in the euphotic zone.

Ammonia values tended to show sporadic increases during 1970, and at times ammonia may have been the principal inorganic form of nitrogen in the lake, probably through being recycled as excretory products of the zooplankton (Beers, 1962). However, due to analytical difficulties with this radical, further investigation of its seasonal behavior is required, especially with reference to the verification of high values. Phosphate showed similar variations to nitrate although the depletion of phosphate was less regular. Seasonal concentrations ranged from <0.01 to 0.04 μg at. P/liter with about 3% of the values falling in a much higher range of 0.1 to 0.6 μg at./liter. A determination of phosphate utilized and phosphate added (similar to the inorganic N budget shown in Figure 7) was difficult to describe because of the unpredictable occurrence of phosphate throughout the summer; this may have been due to phosphate regeneration. As an overall assessment, however, if a winter level of 0.03 μg at. P/liter were completely utilized in the water column 0 to 30 m, the addition of 100 tons of 27-14-0 would increase the supply of phosphate over the whole lake by a factor of about 450% compared with the increase in the inorganic nitrogen budget of approximately 100% (Figure 7).

From winter to summer, silicate concentrations ranged from about 1.8 to 3.0 mg silica/liter. According to Lund (1965) silicate becomes rate limiting for diatoms at about 0.5 mg/liter, which is considerably lower than the seasonal range for Great Central Lake.

BACTERIA

Plate counts of bacterial colonies per 100 ml are shown in Figure 8, together with the range of counts obtained on several days when areal surveys were made. During May, the total number of colonies per 100 ml was generally below the mean value of ca. 9,000 reported by Henrici (1940) for oligotrophic lakes; however, there is

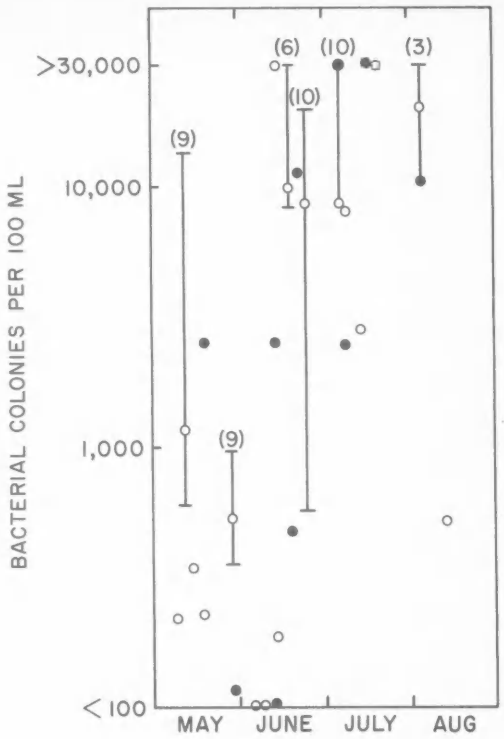

FIGURE 8.—Bacterial colonies per 100 ml surface lake water (○) Station 2; (●) Station 1; (5) number of samples in areal survey and range, I.

some indication in the data that bacterial numbers increased by one or two orders of magnitude during the latter part of June through to August. Summer increases in bacterial flora have been widely observed in lakes (e.g., Snow and Fred, 1926; Nauwerck, 1963), and while nutrient level could have affected this increase (e.g., see Bosset, 1965), we have no previous data on which to judge the effect.

PHYTOPLANKTON SPECIES

Principal phytoplankton species from surface samples at Station 1 and 2 during 1970 are shown in Figure 9 on a relative scale. From these results it is apparent that the predominant algae during May and early June were *Dinobryon, Rhizosolenia,* and *Nitzschia.* During June and July *Gymnodinium, Cyclotella,* and the euglenoid *Phacus* reached maximum numbers but tended to decline by August. Predominant algae of late summer and autumn were the chlorophyte *Nannochloris* and the cyanophyte *Chroococcus.* Second maxima in *Dinobryon, Rhizosolenia,* and *Cyclotella* occurred during the winter together with a maximum in *Tabellaria.*

Two studies (May and June) on the depth distribution of the principal species showed that maxima in *Rhizosolenia, Tabellaria,* and *Phacus* were found at the bottom of the thermocline (ca. 20 m); *Cyclotella* and *Gymnodinium* maxima occurred at the top of the thermocline (ca. 10 m) while *Nannochloris, Dinobryon, Nitzschia,* and *Chroococcus* showed maxima within the top 0 to 10 m.

PRIMARY PRODUCTION

Surface primary production values at Station 1 during 1969 and 1970 and at Station 2 during 1970 are shown in Figure 10; the mean and coefficient of variation of surface primary production for the months of June to August are also shown on each figure. The total average primary production in the water column 0 to 30 m at Stations 1 and 2 during 1970 was approximately 12 g C/m²/year compared with approximately 6 g C/m²/year at Station 1 during 1969.

Primary production per unit of chlorophyll *a* at different depths for Station 1, 1969 and 1970, and Station 2, 1970, are shown plotted against the light intensity at the same depths in Figure 11. A considerable amount of scatter is apparent in the data which is partly due to differences in environmental factors as well as to the lack of precision in attempting to establish photosynthesis versus light intensity relationships on the basis of ecological rather than experimental data. Polynomial curves were fitted to each set of data using an IBM computer. The shape of these curves is consistent with P vs. I relationships obtained by physiologists under experimental laboratory conditions and differences in asymptotic values reflect differences in the nutrient supply (Ichimura and Aruga, 1964).

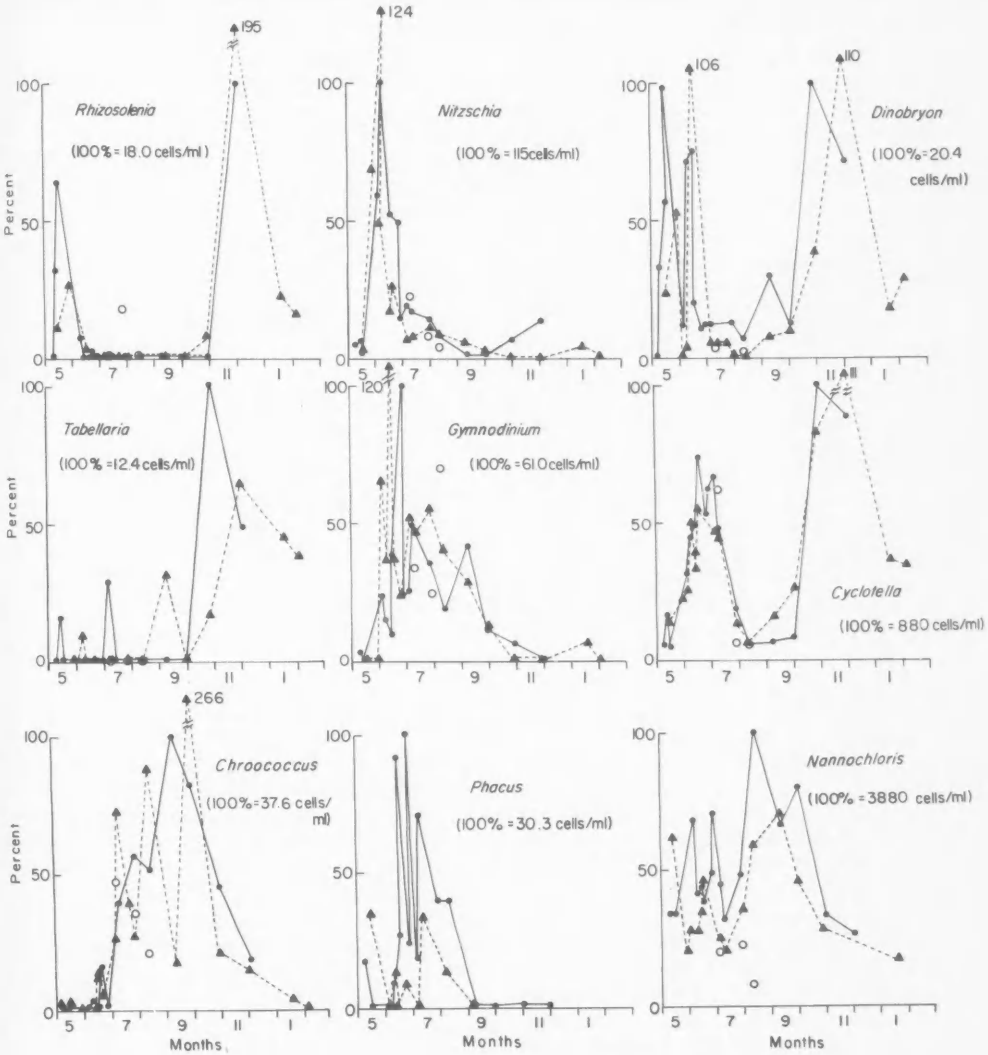

FIGURE 9.—Principal phytoplankton species at Station 1 (●), Station 2 (▲), Station 3 (○) during 1970.

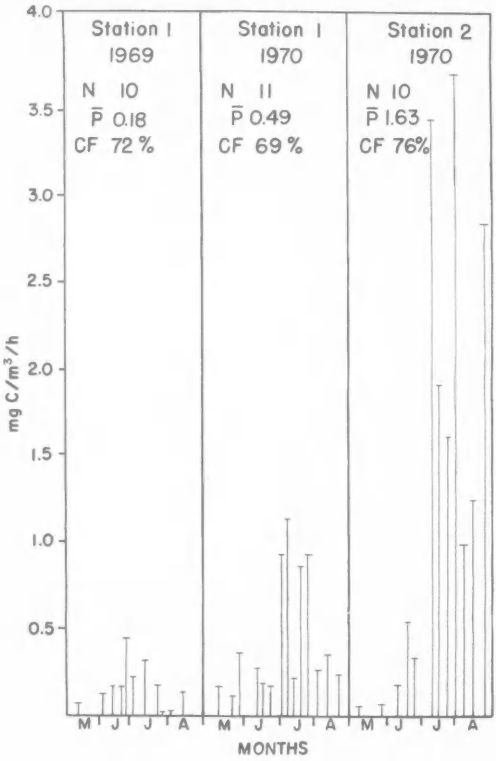

FIGURE 10.—Surface primary production, May to August. (N = number of samples, $\bar{P}$ = mean surface production, and CF = coefficient of variation—all values for the period, June to August.)

However the degree of scatter in the ecological data requires some expression of confidence limits. At Station 1 (1969), which was located at a considerable distance from the area of fertilization, 95% confidence limits for the asymptotic value of 1.03 mg C/mg Chl *a*/hr were 0.84 and 1.22; for 1970 at the same station the 95% confidence limits for the asymptotic value of 1.55

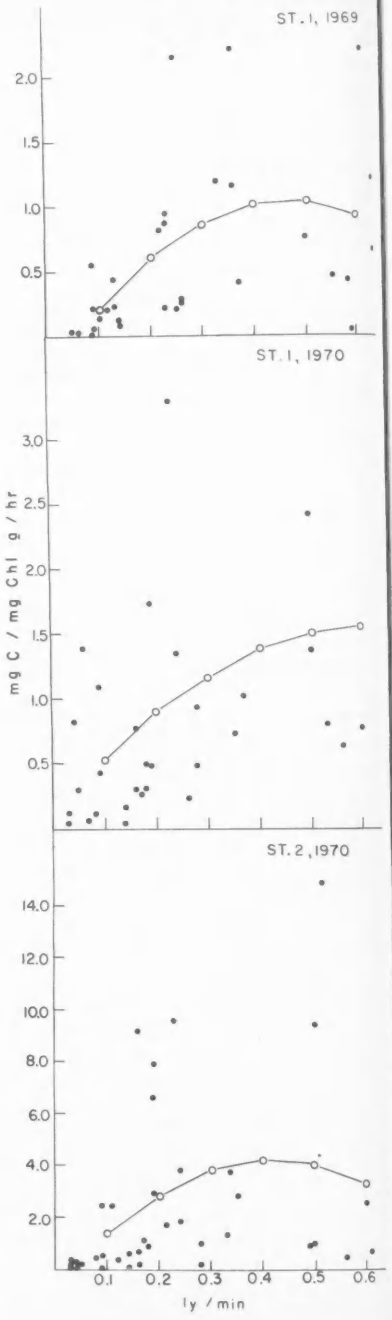

FIGURE 11.—Productivity indices plotted against light intensity at Station 1, 1969 and 1970, and Station 2, 1970 (O——O computed best fitting polynomial curve).

mg C/mg Chl *a*/hr were 1.12 and 1.98. At Station 2 in 1970, however, the scatter of points is so great that 95% confidence limits become very large. The probable reason for this is that the station was sometimes in the area to which nutrients were first added, and sometimes the movement of water containing freshly added nutrients was away from Station 2 (Figure 1). If in fact it is assumed that there were only two alternatives in such a narrow lake (i.e., movement of nutrients towards or away from Station 2) then the 50% confidence limits for the asymptotic value of 4.17 mg C/mg Chl *a*/hr were 2.26 and 6.07.

DISCUSSION

The principal purpose of this report is to establish the effect of inorganic nutrient enrichment on the primary production of Great Central Lake. From data in Figure 10 it is quite apparent that primary productivity was increased in surface samples during 1970 compared with 1969, both at Station 1 and particularly at Station 2, which was very close to the area of repeated enrichment. However, while the effect of nutrient enrichment was apparent to the extent of a tenfold increase in surface primary productivity, the integrated productivity for the water column only showed an approximate doubling in primary productivity during the first 3 months of nutrient enrichment (see Parsons et al., in press, for primary production depth profiles). This result is in keeping with the fact that the total inorganic nitrogen addition to the lake (Figure 7) was only sufficient to approximately double the natural reservoir of inorganic nitrogen in the upper 10 m, based on winter nitrate levels. However, it does not take into account nitrogen fixation by the blue-green alga, *Chroococcus*, which may have taken arvantage of the increased supply of phosphate to become one of the predominant summer plankters.

The question is, whether some factor other than fertilization could have accounted for the increased primary productivity? Firstly, it is apparent that since the largest increase in primary productivity occurred at the surface, it cannot be argued that the increased primary productivity was due to greater enrichment of the water column from the hypolimnion, especially in view of the high degree of stratification (Figure 3) and apparent nitrate depletion in the epilimnion (Figure 6). It might be argued that the increased productivity was due to an increase in standing stock of primary producers and increased radiation. Data in Figure 5 indicate that the standing stock of primary producers at Station 2 was generally higher than at Station 1 during 1969, although the effect is within a 95% probability of being due to within-lake variations in standing stock of chlorophyll *a*. However, in order to examine this question in more detail, primary productivity data for Stations 1 and 2 in 1970 and Station 1 in 1969 have been expressed as the production per unit chlorophyll *a* and plotted against the calculated light intensity at various depths (Figure 11). This presentation of data has been used by Ichimura and Aruga (1964) to compare the productivity of oligotrophic, mesotrophic, and eutrophic lakes under conditions of different standing stocks of primary producers, light conditions, and photosynthesis. From their findings it was concluded that oligotrophic lakes had a productive index of between 0.1 and 1.0 mg C/mg Chl *a*/hr, which is very similar to the range of values computed from the data in Figure 11 for Station 1 during 1969. The computed range for Station 1 during 1970 was appreciably higher, however, and enters the classification for mesotrophic lakes which have a photosynthetic index of up to 2 mg C/mg Chl *a*/hr; finally the asymptotic value (4.17) from Station 2 in 1970 is within Ichimura's and Aruga's (1964) range for eutrophic lakes, which the authors report as having photosynthetic indices of up to 6 mg C/mg Chl *a*/hr. Since the only basis for this classification is the effect of nutrient enrichment in enhancing the photosynthetic response, it may be concluded that our observed increase in primary productivity was determined by the artificial addition of fertilizer.

Secondary effects of nutrient enrichment may also have influenced the primary formation of particulate material through a heterotrophic cycle. Unfortunately, our evidence for this is not substantial and rests mainly on the increase

in bacterial numbers (Figure 8) and the fact that very high dark uptake of ^{14}C-bicarbonate (up to 50% of the light bottle uptake) were encountered during the summer at some stations following fertilization. We are at present not sure of the accuracy of this result, however, and it will be reinvestigated during 1971. Nauwerck (1963) has concluded that the heterotrophic formation of particulate material is a principal mechanism for supplying food to particle feeders in some lakes and one might expect this mechanism to be enhanced by the additional availability of nitrogen and phosphorus.

The most interesting aspect of changes in the species composition of the principal primary producers is that in spite of differences in surface primary productivity at Stations 1 and 2 during 1970 (Figure 10) the relative abundance of principal species at these two stations (and on several occasions at Station 3) was substantially the same (Figure 9). This was important because it was intended that there should be no change in the species composition of organisms leading up the food chain to young salmon, but only an increase in their productivity. In addition, the occurrence of the *Cyclotella-Chroococcus* association is characteristic of oligotrophic lakes (Hutchinson, 1967) which indicates that the general classification of the lake (based on species association) had not been changed by fertilization. However, some eutrophic species of phytoplankton, such as *Ceratium*, *Peridinium*, and *Scenedesmus*, were also observed as minor constituents of the plankton, especially during the summer.

In conclusion, it appears that the fertilization of Great Central Lake resulted in an increased primary production but did not substantially change the standing stock of primary producers, water clarity, or the principal phytoplankton species at locations near and distant from the site of nutrient enrichment. The effect of zooplankton on the primary producers was essentially to suppress the increase in standing stock of phytoplankton while the standing stock of zooplankton itself increased by almost an order of magnitude. Zooplankton growth and distribution are described in the second paper in this series (LeBrasseur and Kennedy, 1972).

ACKNOWLEDGMENT

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THE FERTILIZATION OF GREAT CENTRAL LAKE
II. ZOOPLANKTON STANDING STOCK

R. J. LeBrasseur and O. D. Kennedy[1]

ABSTRACT

The regional, vertical, and seasonal abundance of the dominant zooplankton species were studied in conjunction with a series of nutrient additions to Great Central Lake. Two rotifer species, *Kellicottia* spp., *Conochilus unicornis*, three cladocera species, *Bosmina coregoni*, *Holopedium gibberum*, and *Daphnia longiremis*, and three copepod species, *Cyclops bicuspidatus thomasi*, *Epischura nevadensis*, and *Diaptomus oregonensis* were the most numerically abundant zooplankton species. The introduction of the fertilizer and the consequent higher rate of primary production produced no changes in the species composition. The zooplankton exhibited a relatively uniform horizontal distribution within the upper 20 m along the lake, a factor which was attributed to the lake circulation. All eight species were concentrated in the euphotic zone (upper 40 m), and five were most abundant in the upper 10 m. The center of abundance for the remaining three species was between 20 and 30 m depth. The respective depths of maximum abundance for the various species showed little variation between daylight and darkness. Seasonally, there were two periods, June to July and September to October, of maximum abundance for most species. The cause for somewhat lower levels of abundance in August is not known. The average zooplankton biomass showed a similar seasonal pattern with a maximum weight in July which exceeded 8 g/m^2. The average biomass over a 6-month period, May through October, exceeded 5 g/m^2 (more than 10 times greater than for the comparable period prior to fertilization in 1969). In contrast to the high standing stock of zooplankton, the estimated growth rate for underyearling sockeye salmon, the principal predator species in the lake, was only slightly improved over 1969 (1.2 vs. 0.9%/day). In comparison with other lakes producing young salmon the growth rates appear low with respect to the zooplankton stock. It was suggested that the temperature structure of the lake, 14° to 23°C above the thermocline and 4° to 6°C below the thermocline, may reduce availability and prevent the efficient utilization of the zooplankton by the underyearling sockeye salmon.

The following account is the second in a series of papers which report on the effects of sustained nutrient additions to an oligotrophic lake. In the first report, Parsons et al. (1972) showed that an increased primary productivity resulted from nutrient additions made to Great Central Lake, B.C.; the objective of this report is to determine if nutrient additions affected the standing stock and diversity of secondary producers.

The overall purpose of these studies has been to determine if nutrient additions will increase sockeye salmon (*Oncorhynchus nerka*) production; zooplankton, as the principal food of underyearling sockeye salmon, occupy a central position in the food chain of young sockeye during lake residence. Previous studies (Ivlev, 1961; Johnson, 1965; Brocksen et al., 1970) have suggested that prey density and availability may limit the predator biomass. The latter authors compiled data for several sockeye nursery lakes with which they were able to demonstrate a direct relationship between mean zooplankton biomass (prey) and the mean growth rate and biomass of underyearling sockeye salmon (predator). Other studies (Ricker, 1962) have indicated that the ocean survival, i.e. the return to coastal waters of adult sockeye salmon, can be directly correlated in many instances with the size at which the sockeye as year-old migrants leave the nursery lakes to enter the ocean for 2 or more years. While the above studies rely heavily upon circumstantial data, as well as data which were collected for other purposes, they serve as a rational basis for attempting to increase the available zooplankton biomass for the enhancement of salmon growth.

[1] Fisheries Research Board of Canada, Biological Station, Nanaimo, B.C., Canada.

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METHODS

Sampling of zooplankton was initiated in mid-1969, using a 0.25 m^2 mouth area cylinder-cone net with 100 micron mesh aperture, hauled vertically from 20 m or 50 m. The samples were collected at infrequent intervals during 1969 and the first 14 weeks in 1970; thereafter vertical net hauls were made at two locations at least once every 4 days until the first week of November. Additional vertical net hauls were made once or twice each month from the lake bottom, 200 m, to the surface. Miller nets (Miller, 1961) with 0.01 m^2 mouth area and 100 micron mesh aperture were used at weekly intervals during the period June through August and thereafter at monthly intervals to determine the areal and vertical distribution of zooplankton. The areal sampling at 18 locations along the lake consisted of 5 min oblique tows from 20 m to the surface while underway at 2 m/sec. The daylight vertical distribution of zooplankton was monitored at 18 depths between the surface and 65 m by making three consecutive tows each with six Miller nets at 2 m/sec at one location. Additional tows were made to sample other depths and also at other periods of the day. Details of the sampling and sampling locations are reported elsewhere (Kennedy et al., 1971[2]).

In the analyses of samples special effort was made to maintain up to date species counts and measurements for comparison with other events as they were occurring in the lake. The common zooplankton constituents were identified, measured into size categories, and counted from an aliquot of the total sample; fractions of 1/50 or 1/100 using a Stempel pipette were used depending upon the sample size. The size categories (length in microns) reported in Table 1 were based upon individual measurements for different stages of development of the respective species. It is to be noted that the lengths refer to mean sizes of organisms during the spring and summer growing period. Individual length measurements for the different species and for different times of the year may be found in the MS data report (see footnote 2).

Species counts in vertical net hauls are reported as number per m^2, in oblique and horizontal tows as number per m^3. In this report, unless otherwise indicated, counts all refer to numbers of individuals which fall within the size range occupied by mature (Stage VI) copepods and egg-bearing cladocera; these were usually the two largest size groups for the species reported in Table 1.

RESULTS

SPECIES

Table 2 lists the species of zooplankton which have been found in Great Central Lake. Additional species may be present as minor constitu-

[2] Kennedy, O. D., K. Stephens, R. J. LeBrasseur, T. R. Parsons, and M. Takahashi. 1971. Primary and secondary productivity data for Great Central Lake, B.C., 1970. Fish. Res. Board Can., Manuscr. Rep. No. 1127, 379 p.

TABLE 1.—Zooplankton size ranges for species sorting in Great Central Lake.

Species	Group						
	I	II	III	IV	V	VI	VII
	Size range μ						
Cyclops bicuspidatus	Egg	125-275	375-550	550- 750	750- 850	850- 950	950-1,100
C. vernalis	Egg	275-375			750- 900	900-1,100	1,100-1,350
Epischura nevadensis	Egg	275-450	450-650	650- 900	900-1,100	1,100-1,350	1,350-2,250
Diaptomus oregonensis	Egg	125-275	450-750	750- 900	900-1,100	1,100-1,350	
D. kenai	Egg			650-1,100	1,100-1,750		1,750-2,500
Bosmina	Egg	125-225	225-325	325- 450	450- 650	650- 800	
Holopedium	Egg	375-450	450-750	750-1,100	1,100-1,750		
Daphnia longiremis	Egg	450-750	450-750	750-1,100	1,100-1,750		
D. pulex	Egg	450-650	450-750	750-1,100	1,100-1,750	1,750-2,500	
Kellicottia	Egg	ca. 80					
Conochilus	Egg	ca. 80					
Keratella	Egg	ca. 80					

TABLE 2.—Zooplankton species found in Great Central Lake, 1970.

Rotifera	Copepoda
**Kellicottia* spp.	**Cyclops bicuspidatus thomasi*
Keratella cochlearis	*C. vernalis*
K. quadrata	**Epischura nevadensis*
**Conochilus unicornis*	**Diaptomus oregonensis*
	D. kenai
Cladocera	**Unknown**
**Bosmina coregoni*	Actinopoda
**Holopedium gibberum*	Pollen
**Daphnia longiremis*	Egg clusters
D. pulex	Arachnoidea (mites—2 spp.)
Scapholeberis kingi	Chironomid larvae
Polyphemus pediculus	Fish larvae (cottid)
Alona affinis	

* Indicates the most common species.

ents of the zooplankton and it is also possible that new species are being introduced into the lake through a hydroelectric installation which discharges water from an adjacent watershed into the lake. It will be noted from Table 2 that the common zooplankton constituents consisted of two rotifer species, three species of cladocera, and three species of copepods; these species are identified throughout the text by their generic names. There has been no change in the species composition during the course of the experiment, i.e. the common species have remained numerically abundant while the rare species have continued to occupy a minor role.

PATCHINESS

It was anticipated that the zooplankton would exhibit contagious distributions reflecting local circulation patterns, species preferences, and predation. Accordingly, oblique samples from 20 m were collected at weekly intervals at 18 positions along the lake, both near the shore and in midlake. In general, with the exception of the area near the inlet and outlet of the lake where the abundance of organisms was sometimes low, there was greater variability found with respect to the date of sampling than the location of sampling. Weekly means and standard deviations computed for each species showed that *Cyclops* was the only species in which the standard deviation exceeded the weekly count for more than half the surveys (11 out of 17). The apparent variability in *Cyclops* abundance might be due contagion or, more likely, to the fact that sampling was limited to depths (20 m) where *Cyclops* were seldom abundant (see section on vertical distribution). The major source of variability in weekly mean counts appears to be associated with the number of organisms counted, i.e. the number of organisms in a sample and the size of the aliquot counted. The weekly mean number of organisms for each species were grouped together with their respective standard deviations as follows: 1-50, 51-250, 251-500, 501-1,000, 1,001-2,000, 2,001-5,000. The mean coefficient of variation (C.V.), the range, the number of means present in each group, and the number of times a standard deviation exceeded its respective mean are shown in Figure 1 (e.g. for 50 or fewer organisms counted, the standard deviation in 17 out of 23 samples exceeded the mean). The magnitude of C.V., or the relative variation about a mean, is closely associated with the number of organisms counted. The high degree of variability about a mean of 50 or fewer organisms reflects counting errors due to the subsampling technique used in the initial analyses of the samples. However, counts of organisms of 250 or more per m^3 tend

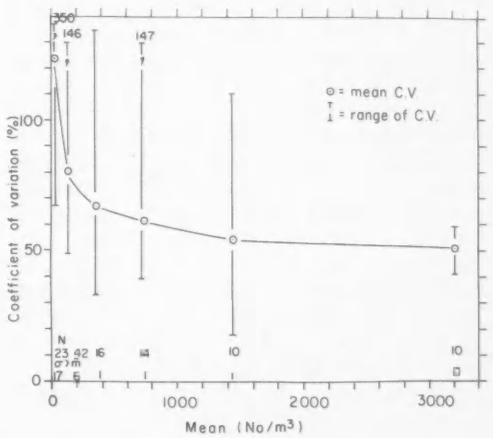


FIGURE 1.—Coefficient of variation computed for mean counts of species sampled in oblique (20 m to surface) tows, where N is the number of weekly means, $\bar{m}$ and σ is the standard deviation.

to be relatively uniform, suggesting that horizontal patchiness or local contagion is not a typical feature of Great Central Lake zooplankton. The observations of lake circulation (McAllister, personal communication) (Parsons et al., in press), and the chlorophyll *a* distribution (Parsons et al., 1972) confirm that the epilimnion is well mixed, thus assuring a nearly uniform dispersal of planktonic organisms along the lake.

The 50-m vertical hauls made at Stations 1 and 2 provide further opportunity for examining the variability with respect to different sampling locations. Here, the comparisons of *mean* counts indicated a high degree of similarity between the two locations with respect to species composition, stage of development, and abundance. However, examination of samples collected on the *same day* indicated a high degree of variability. Forty-nine samples were collected from Stations 1 and 2 during May through December; species counts for Station 1 were plotted against the respective count for Station 2. Values which fell outside of a mean $\pm$ half the expected mean (where the expected mean equals half the counts for Stations 1 and 2 combined) are tabulated in Table 3. On half the sampling dates the counts for a particular species tended to be similar at both locations (e.g. in the first column of Table 3, the number of samples with a mean $\pm\ m/2$ is generally greater than half the total number of samples, $N/2$). Greater numbers of four species were found at Station 2 than at Station 1. It is noteworthy that three of the four species, *Kellicottia*, *Cyclops*, and *Daphnia*, have their greatest abundance below the epilimnion at depths greater than that sampled on the areal surveys. However, there was no apparent correlation in the relative abundance of any of these three species with respect to each other or to other species at either station.

There were, however, periods when three or more species would be more abundant at one position than at the other. For example, from July 3 to July 21 (six sets of samples) three to six species were most abundant at Station 1 while during the period August 21 to September 8 (six sets of samples) three to seven species were most numerous at Station 2. Similarly, for other periods of 4 to 12 days, one or another species was in greater abundance at one station than the other.

These data have not been examined further to show if variation in species abundance between sampling positions can be correlated with variations in the lake circulation or other environmental factors such as fertilization or predation by underyearling sockeye. However, it is apparent that all seasonal changes in species composition and abundance were reflected throughout the near-surface waters of the lake and that no local area of high or low zooplankton concentration could be clearly defined within the main body of the lake.

TABLE 3.—Comparison of counts of zooplankton from 50-m vertical hauls at Stations 1 and 2, $N = 49$.

Species	Counts $= (m \pm \frac{m}{2})$	Station 1 $>(m + \frac{m}{2})$	Station 2 $<(m - \frac{m}{2})$
Cyclops	33	5	11
Epischura	31	10	8
Diaptomus	24	10	15
Bosmina	26	17	6
Holopedium	25	15	9
Daphnia	22	6	21
Kellicottia	24	9	16
Conochilus	29	14	6

VERTICAL DISTRIBUTION

Horizontal tows made within the upper 60 m revealed marked differences in species composition and abundance with depth during the period of thermal stratification. As an example the weekly tows made during July were combined and the average concentration of each species at each of 17 depths sampled during daylight is shown in Figure 2. The inset associated with each species distribution shows the relative distribution (25% quartile intervals) of the respective populations sampled during a 24-hr period in August.

Five of the eight species shown in Figure 2 have their maximum concentration within the upper 10 m, while the maximum concentration of the other three species was below 20 m. Thus the species maxima fall either above or below the thermocline. However, it should be noted that the number of organisms per m^3 decreased from a maximum of greater than 7,000/m^3 be-

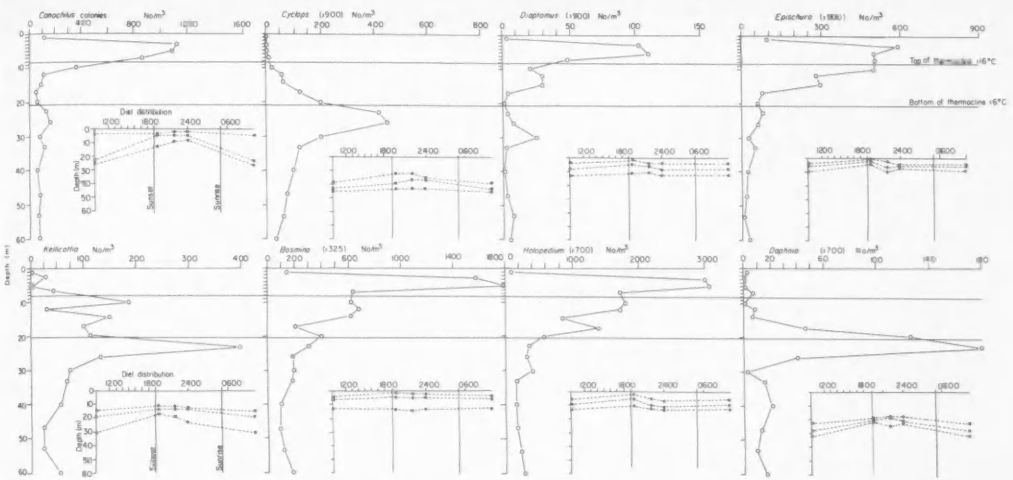


FIGURE 2.—Vertical distribution of common zooplankton species in Great Central Lake mean no./m³ for July 1970. (Horizontal lines indicates the top and bottom of the thermocline, McAllister (personal communication). Inset shows the vertical distribution at 25% quartile intervals over a 24-hr period. Note: the scale indicating the quantity of organisms varies for each species.)

tween 3 m and 5 m to a minimum of approximately 500/m³ at depths below 40 m. The maximum concentration of individual species ranged from 180/m³ for *Daphnia* to greater than 3,000/m³ for *Holopedium*. The tendency for some species to show an increase in abundance in deep samples was likely due to contamination from shallower depths since in the process of setting and hauling with nonclosing nets the deeper nets actually sample for a slightly longer time than the shallower nets. Variations in abundance with respect to time of sampling was noted for all species (Figure 2 inset). The effect was generally most pronounced just after sunset when the maximum concentration per m³ of a species might be increased by 30%. Rotifers, which were presumably the least motile of the zooplankton, exhibited the largest shift in abundance towards the surface with the onset of darkness. Some species, notably *Holopedium* and *Epischura*, returned to their daylight depth of maximum abundance within 2.5 hr after sunset. Other species, such as rotifers, *Bosmina*, and *Daphina* exhibited relatively little movement during darkness. It is apparent from Figure 2 that the shift in species abundance were all within the daylight range occupied by the bulk of the respective populations. Furthermore, more than 75% of the zooplankton populations were at all times within the euphotic zone (i.e. surface to 30-40 m).

SEASONAL ABUNDANCE

In Figure 3 the mean monthly numbers of zooplankton are shown for the 50-m vertical haul samples. Three species, *Cyclops*, *Bosmina*, and *Kellicottia*, were relatively abundant throughout the year, whereas the other species were present in numbers which exceeded 1,000/m³ for periods of 4 to 5 months. *Conochilus* were the only species present during 1970 to appear subsequent to the initiation of nutrient addition. (They were present in 1969 samples.) *Cyclops* ranged from a winter minimum of 2,000/m² to a maximum in September and October of 30,000/m². *Epischura* were never numerically dominant but ranged in numbers from 2,000 to 4,000/m² from May through September. Counts of *Diaptomus* did not exceed 1,000/m² until August, but by September there was a

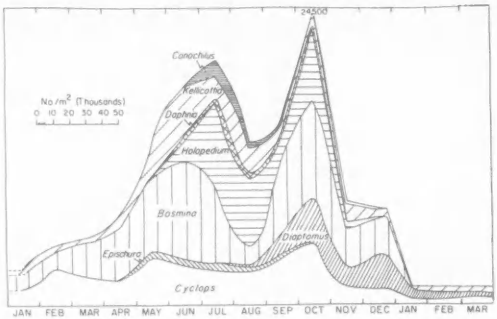


FIGURE 3.–Monthly mean zooplankton abundance (no./m² in the upper 50 m data from Stations 1 and 2 combined).

7-fold increase which in turn doubled to ca. 26,000/m² by October. The November-December catches of *Diaptomus* exceeded 10,000/m², which was approximately two orders of magnitude greater than their standing stock 12 months earlier. Substantial numbers of *Diaptomus*, 3,000 to 4,000/m², were carried through into 1971. *Bosmina* were the most abundant species collected throughout the year. Their numbers ranged from ca. 8,000/m² in January to ca. 60,000/m² in June and again in October. The December concentrations of *Bosmina* were twice that of the preceding January. However, by January of 1971 *Bosmina* had virtually disappeared from the water column, 0 to 50 m. *Holopedium* attained their maximum abundance in July, approximately 3 months after they began appearing in the samples in significant quantities, i.e. greater than 1,000/m². Following a secondary maximum in October, *Holopedium* were virtually absent from samples collected from December through March. *Daphnia* were the least numerous of the zooplankton species routinely sampled. They occurred in numbers of 1,000 to 3,000/m² from June through September. *Kellicottia* exceeded 10,000/m² from May through August and again in October and November. Nearly twice as many *Kellicottia* were present in December as were present at the beginning of 1970. The maximum abundance of *Conochilus* colonies (2,000/m²) was during July; no colonies were found prior to June and by December the number of colonies had declined to approximately 500/m².

In toto there were two to three times more zooplankton present in December of 1970 than there were the preceding January. It is of interest to note that the greater abundance of zooplankton at the end of 1970 was not maintained through the first 3 months of 1971 and further, that *Bosmina* had been apparently supplanted by *Diaptomus* in 1971. On a monthly basis there were fewer than 22,000 organisms/m² in January while in October, where the maximum concentration was observed, there were nearly 10 times as many organisms present. Zooplankton counts exceeded 100,000/m² in June, July, September, and October. The decrease in zooplankton abundance in August was approximately 15% lower than that in either July or September; this decline was attributable mainly to fewer numbers of *Bosmina*.

Individual species counts (4-day running mean number/m²) in vertical hauls have been presented in Figure 4 in order to show the seasonal variations in abundance in greater detail than is shown in Figure 3. The general features of both figures are the same but in Figure 4 the rapid increase and decrease in numbers of some species are shown more clearly, e.g. *Holopedium* and *Epischura*. From Figure 4 it is possible to infer some relationship between the addition of nutrients and the appearance of *Conochilus* or the sustained increase in the abundance of *Diaptomus*. It is noteworthy that all species, with the exception of *Epischura* and possibly *Daphnia*, went through a secondary maximum in October which was nearly as great as or greater than their level of abundance earlier in the summer.

SEX RATIO

Adult stages of *Cyclops* and *Epischura* showed marked imbalances from an expected 50:50 ratio of females to males through the year (Table 4). Males of these two species were clearly predominant during the late winter and early spring months. *Cyclops* females were predominant among the adults taken in June through August whereas *Epischura* females were never numerically dominant for more than two or three sampling periods, i.e. July 21 to 31, August 28 to

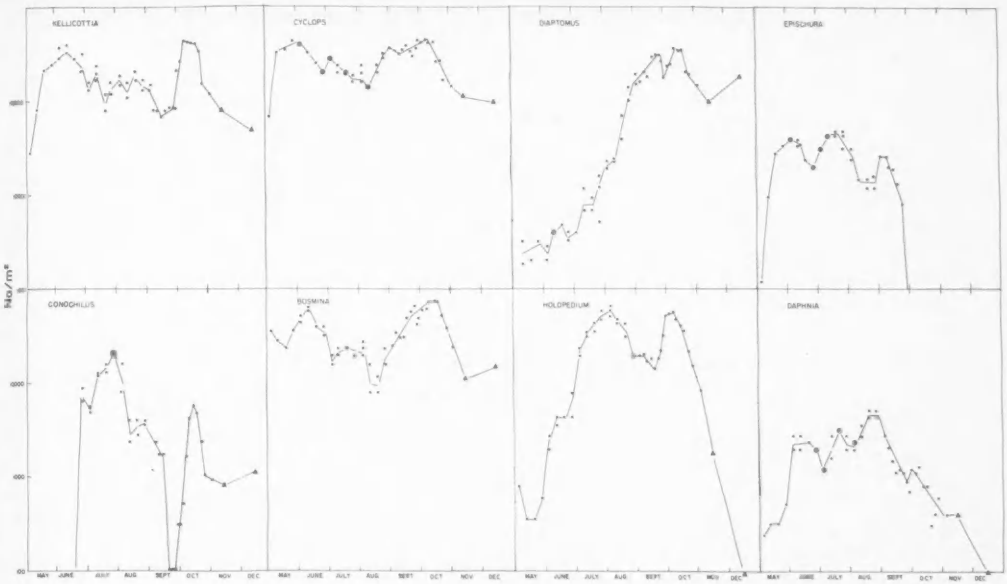


FIGURE 4.—Species counts (no./m² in 50-m vertical hauls at Stations 1 and 2. (Points represent a 4-day running mean, solid triangle indicates monthly mean, circle with dot indicates more than one sample with the same count. Note: the numbers of organisms are shown on a logarithmic scale.)

TABLE 4.—Copepod sex ratios.

Month	Species					
	Cyclops		*Diaptomus*		*Epischura*	
	F/M	F_2/F_1	F/M	F_2/F_1	F/M	F_2/F_1
Jan.-April	0.6		1.2		0.5	
May	0.6	2.8	1.5	0.7	0.7	1.3
June	2.6	1.1	1.1	1.9	0.7	1.4
July	1.9	1.0	1.5	1.1	1.0	1.1
Aug.	1.9	1.6	1.3	1.0	1.1	0.8
Sept.	0.8	2.2	1.2	0.9	1.4	0.9
Oct.-Dec.	1.0	2.0	1.3	0.9	1.0	0.5

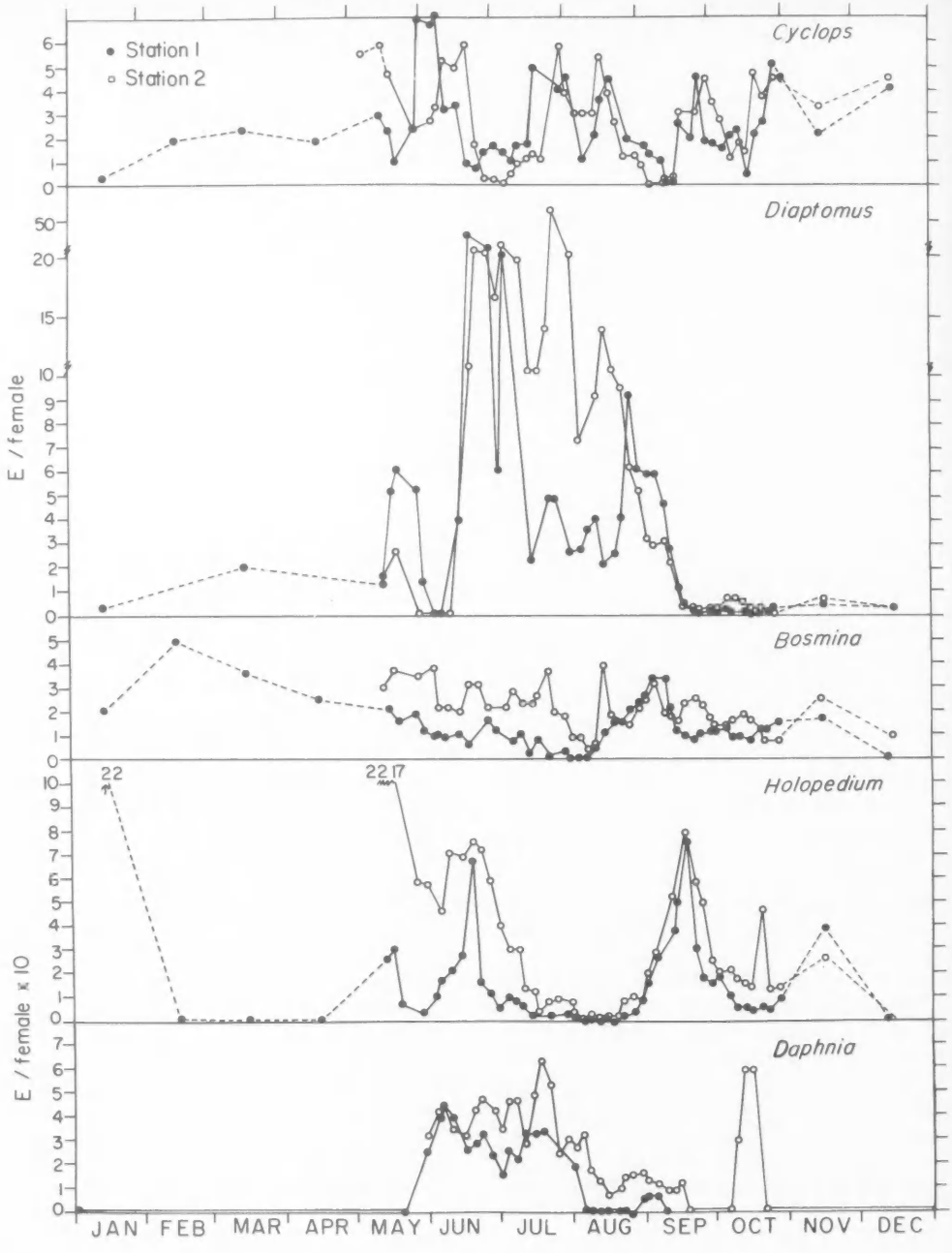
F/M Number of adult females/number adult males.
F_2/F_1 Number of adult females at Station 2/number of adult females at Station 1.

September 14. In contrast there was a tendency for *Diaptomus* females to be slightly more abundant than males throughout the year. The only period for which *Diaptomus* males were consistently more numerous than females was from June 22 to July 10. Included in Table 4 is the ratio of the number of female copepods at Station 2 to the corresponding number at Station 1. *Cyclops* was the only species in which the females were as numerous or more numerous at Station 2 than at Station 1.

EGG PRODUCTION

Counts were made of all readily identifiable eggs; these consisted of eggs in the brood pouch of cladocera and the egg sacks of *Cyclops* and *Diaptomus*. Rotifer species were not examined for eggs, while *Epischura* eggs were positively identified on only one occasion from a horizontal tow made at 1 m depth in August. It is possible that *Epischura* eggs develop close to the surface at depths of less than 1 m since they were not found at other standard depths sampled between 1 m and 65 m. Also other data, not presented here, indicate that the smaller size groups of *Epischura* were found closer to the surface than the adult stages.

The data presented in Figure 5 show the ratio of eggs per female for vertical samples collected at Station 1 and Station 2. It was noted in Table 4 that maximum numbers of copepod females occurred during the summer, June through September; *Cyclops* females were more numerous at Station 2 than Station 1 and *Diaptomus*


Cyclops
Station 1
Station 2
Diaptomus
E / female
Bosmina
22
22 17
Holopedium
E / female x 10
Daphnia
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC

females were in about equal numbers at both stations. In Figure 5 the eggs per *Cyclops* were about equally numerous at both stations. There were three and possibly four periods of maximum egg production for *Cyclops* females, i.e. June, mid-July through to the third week in August, and the last week of September through to the first week of November; the latter time interval could possibly be interpreted as consisting of two separate periods of egg production (late September and late October). *Diaptomus* females at Station 1 had two major periods of egg production, mid-June through mid-July and mid-August through the first week of September, with a period of relatively low egg production from mid-July to the end of August. At Station 2 there was no clear cessation of *Diaptomus* egg production from mid-June through to the first week of September. For a major part of this period there were more than 10 eggs per female being produced. There was also a brief period of *Diaptomus* egg production in mid-May.

The production of *Bosmina* eggs ranged between 0 and 0.5 per individual. From May through mid-August more eggs were produced at Station 2 than at Station 1 and thereafter the egg production was nearly equal at both stations. The summer minimum which occurred in the first 2 weeks of August was followed by a rise in the number of eggs in the first week of September continuing until the end of the third week of September. The summer maximum of adult *Bosmina* shown in Figure 4 occurred approximately 1 week after that of the eggs while the maximum standing stock of *Bosmina* (which occurred in mid-October) was preceded by the production of eggs 3 to 5 weeks earlier. *Holopedium* exhibited two clearly defined peaks in the production of eggs, from the first to the third week of June and again from the first to the third week of September. The corresponding maximum in the standing stock of *Holopedium* shown in Figure 4 occurred from the second week of July through to August 25 and from September 27 to about October 20; the summer minimum occurred between the two peaks. The production of *Daphnia* eggs took place from June to mid-September with a second brief rise in egg production during mid-October at Station 2. The numbers of eggs produced per female at Station 2 by all species of cladocera was generally greater or equal to that at Station 1. It should be noted that the latter was found for both the prefertilization period in May as well as during the period of nutrient additions.

FIGURE 5.—Ratio of the number of eggs to the number of adult females. The data from 50-m vertical samples at Stations 1 and 2 have been averaged to give a 4-day running mean ratio. Note: scale changes for different species.

ZOOPLANKTON BIOMASS

The wet weights for 1970 50-m vertical hauls at Stations 1 and 2 were combined and expressed as a monthly mean wet weight (g/m^2) together with the range about the mean weight (Figure 6). Included in Figure 6 (below) are individual weights for the 1969 sampling. The maximum wet weight in 1969 never exceeded 1 g/m^2 whereas in 1970 the weights ranged as high as 15 g/m^2. The average wet weight of zooplankton during the period May through October was approximately 0.5 g during 1969; for the same period in 1970 the average weight was 10 times larger, i.e. 5.3 g. The sample weights increased at a rate of 3% per day May through July to a maximum average wet weight of 8.6 g/m^2; there-

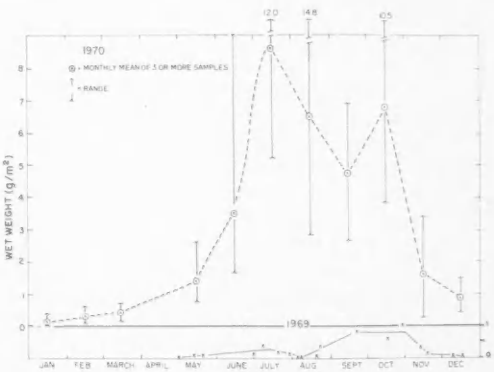


FIGURE 6.—Zooplankton wet weight (g/m^2) for 50-m vertical hauls. In the lower part of the figure, the points marked "x" indicate individual weights (g/m^2) for 1969 samples.

after the weights declined at an average rate of 1.5% per day to the December biomass of 0.9 g/m². The actual rate at which the mean weight of zooplankton declined in any one month following July was greater than the average computed above due to the increase in biomass in October. Inspection of Figures 3 and 4 indicates that the decline in biomass seen in August was a result of fewer numbers of *Epischura*, *Bosmina*, and *Holopedium*. *Epischura* never reached its earlier level of abundance after August and was virtually absent from the samples by October whereas most other species, *Daphnia* excepted, showed an increase in abundance in October which gave rise to the October increase in biomass.

Dry weights of Great Central Lake zooplankton (determined by the freeze-dry method) ranged from 14% to 26% of the wet weight with a mean of 19%. The variation in the percentage dry weight was directly attributable to the species composition of a sample. For example, the dry weight of *Holopedium* was 14% of their wet weight, whereas the dry weight of *Cyclops* was approximately 26% of the wet weight. The average dry weights of the summer zooplankton (May through October) integrated over a 25-m column, i.e. the depth range in which most zooplankton were concentrated, for 1969 and 1970 was 4 mg and 40 mg/m³ respectively (from Figures 2 and 6).

TABLE 5.—Length-weight measurements of adult crustaceans.

Species	Mean length (Microns)	Wet weight (Micrograms)
Cyclops	960	6
Diaptomus	1,100	11
Epischura	1,500	66
Bosmina	300	4
Holopedium	900	17
Daphnia	900	10

Length-wet weight determinations were made for different sizes and stages of the common crustacean species and the data are summarized in Table 5. The data in Table 6 were obtained by multiplying the maximum concentration (no./m³) of a species within particular depth intervals (Figure 2) by their respective weight from Table 5, thereby providing a measure of biomass with depth. Included in Table 6 are the mean July temperatures within the respective depth intervals. Nearly 60% of the total biomass occurs in the upper 10 m where the mean temperature was about 18°C. In the thermocline, from 10 to 20 m, with a temperature range from 12° to 6°C (mean temperature, 9°C) the biomass was about 50 mg/m³ or approximately 30% of the total. From 20 to 30 m depth the biomass was about 8% of the total. The remaining 3 to 4% of the total biomass occurred below 30 m (30 to 60 m). While these data were derived from July sampling it should be noted that the general distribution of the biomass with depth was similar throughout the period of thermal stratification, i.e. June to October.

DISCUSSION

The zooplankton standing stock in 1970 shows a phenomenal increase over 1969. This can be largely attributed to the affect of the nutrient additions upon the rate of primary production. The results of Parsons et al. (1972) demonstrate a marked increase in the rate of primary production within the upper 5 m; at the same time there was little or no change in the standing stock of primary producers. While experiments and observations of a direct relationship between particular species of primary and secondary producers have not been attempted, the obvious inference is that the zooplankton through increas-

TABLE 6.—Relative biomass of July crustacean zooplankton in various depth intervals (from Figure 2).

Depth range (m)	mT °C	Mean maximum biomass (mg/m³)						
		Cyclops	*Diaptomus*	*Epischura*	*Bosmina*	*Holopedium*	*Daphnia*	Total
0-10	18	--	1.3	39.6	7.2	51.0	.1	99.2
10-20	9	1.2	.3	19.8	2.8	28.9	.5	53.5
20-30	6	3.1	.3	4.9	1.2	3.4	1.8	14.7
>30	<5	.6	--	2.3	.7	1.7	.2	5.6

ing stock size were able to utilize the higher rates of primary production.

It is also apparent that the higher biomass in 1970 cannot be entirely attributed to fertilization since the biomass in May (prefertilization) was also higher than any of the 1969 values. However, the nearly continuous production of eggs by most species and the maintenance of an increased standing stock over a 6-month period are indicative of a direct relation between zooplankton and nutrients. It is also noteworthy that there was no change in species diversity.

The techniques employed for wet weight determinations in this study have produced weights which are apparently lighter than would be obtained by other investigators. Wet to dry ratios in the literature suggest that the dry weight is 5% to 10% of the wet weight. Schindler and Noven (1971) employed a ratio of 6%, although their reason for using this particular value is not given; the present results indicate that the dry weight is 19% of the wet weight. Consequently, the present weights could be increased approximately three times for comparison with other studies. Thus in the lakes which range from oligotrophic to eutrophic, listed by the above authors, Great Central Lake has, in terms of its mean summer zooplankton biomass, changed from oligotrophic to oligotrophic-mesotrophic, i.e. 12 mg in 1969 to 120 mg dry weight/m^3 in 1970. In lakes producing sockeye salmon the mean abundance of zooplankton ranges from values which are less than 5 mg dry weight/m^3 to greater than 1 g dry weight/m^3 (Johnson, 1965). The mean concentrations in Great Central Lake have increased from the very low end of the range to values which are commonly reported for some of the larger sockeye producing lakes, e.g., Babine Lake.

Johnson (1965) concluded that there was a general relationship between the rate of growth of underyearling sockeye and zooplankton abundance. However, he also suggested that with increasing fish density food abundance was supplanted by a space effect as a limiting factor. In Great Central Lake the underyearling sockeye in October of 1970 were ca. 30% heavier than fish caught in October of 1969 (Parsons et al., in press; Barraclough and Robinson, 1972). In addition to the increase in weight these authors report (on the basis of the number of adult salmon spawning) that the number of sockeye fry in the lake were from two to five times more numerous than in the previous year. Assuming an initial weight of 120 mg for individual fry of each year the respective rate of growth over their first 200 days of lake residence was 0.9% and 1.2% per day for 1969 and 1970 respectively. The increased growth rate of sockeye in 1970 is less than might be anticipated from the 10-fold increase in zooplankton abundance. Johnson's data (1965) indicated that a population density of 1 fish per m^2 might be the point at which space becomes a factor limiting growth. The maximum estimate of 1×10^7 sockeye in Great Central Lake during 1970 is approximately 1 fish in every 5 m^2. Consequently it appears unlikely that the density of the fish population in Great Central Lake limited their growth.

Among other factors which limit growth of sockeye, Foerster (1968, Figure 45) indicates that temperature has a major affect upon growth and the efficiency with which food is utilized. The optimum temperature for food conversion for sockeye lies between 10° and 15°C. At higher or lower temperatures the efficiency of food conversion decreases, especially at temperatures in excess of 20°C or less than 6°C. The laboratory studies of Brett et al. (1969) with fingerling sockeye support the findings reported above. In their experiments 15°C was found to be the optimum temperature for growth at high rations; however, maximum efficiencies with which a ration was utilized occurred at lower temperatures, e.g. the maximum food conversion efficiency of 40% with a 0.2% increase in fish weight per day occurred at a temperature range of 8° to 10°C and a ration of 1.5% of the fish weight/day. Temperatures between 5° and 17°C were found to provide the laboratory fish the optimum conditions for conversion efficiencies and growth. In Great Central Lake, during their first 200 days of lake residence, the underyearling sockeye concentrate at depths of 50 m or greater during daylight; with the approach of sunset the fish move to shallower depths and by nightfall the major portion of the population

is at depths between 10 and 20 m while some fraction of the population occur in the upper 10 m. This pattern of vertical migrations appears to be repeated daily (Barraclough and Robinson, 1972). Narver (1970) has reported similar vertical movements for sockeye populations in Babine Lake. For the greater part of the day the salmon in Great Central Lake are at temperatures of 4° to 5°C, a somewhat shorter period (ca. 6 hr) is spent at temperatures of 6° to 12°C (10 to 20 m depth) while a relatively brief period (ca. 1 hr) may be spent at temperatures ranging from 14° to 23°C (0-10 m depth). Details of the time actually spent at different depths by the sockeye are reported by Barraclough and Robinson (1972). It is apparent that the fish are utilizing the maximum concentrations of prey which occur at above optimum temperatures in the upper 10 m for very short intervals. Consequently in assessing the relationship between the increased abundance of prey brought about through fertilization and the sockeye it should be noted that possibly 60% of the total biomass, i.e. the portion in the upper 10 m, may be only partially available to the fish (Table 6). Furthermore, some prey species because of their size (rotifers) or structure (*Holopedium*) may not be a particularly useful food source for the salmon. *Holopedium*, for example, was among the largest and most numerous species of crustaceans in the lake; however, a large fraction of their biomass is comprised of a gelatinous material of dubious food value. The difference in the wet to dry weight ratio between *Holopedium* and other zooplankton (14% to ca. 26% respectively) attests to the water composition of *Holopedium*. The quality of prey together with the observations of Foerster (1968) and Brett et al. (1969) emphasize the need for caution in interpreting predator-prey relations. In the present instance, the benefits of the fertilization appear to have been only partially transferred to the sockeye salmon. Since the thermal structure of the lake is a factor beyond immediate control, it would be interesting to consider possible benefits from the addition or deletion of some prey species and to attempt to shift the level of primary and secondary production to depths and temperatures favoring sockeye salmon growth.

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THE FERTILIZATION OF GREAT CENTRAL LAKE
III. EFFECT ON JUVENILE SOCKEYE SALMON

W. E. Barraclough and D. Robinson[1]

ABSTRACT

Nutrient levels and rates of primary production in nursery lakes are factors which may limit production of sockeye salmon. This paper describes the effect of artificial fertilization on feeding behavior and growth of juvenile sockeye salmon in Great Central Lake, Vancouver Island, British Columbia. Underyearling sockeye salmon grew 30% larger in 1970 than in 1969 as a result of adding 100 tons of fertilizer to Great Central Lake. The growth pattern for the whole population was complex, however, and the increase in size of juvenile sockeye was not as much as had been expected from the increase in quantity of their food organisms. The fact that the sockeye did not appear to appreciably crop the high epilemnetic concentrations of zooplankton during July and August 1970 may have been partly due to avoidance of high temperatures by the fish.

Decomposing carcasses of anadromous fish, such as the sockeye salmon (*Oncorhynchus nerka*), contribute to the fertilization of nursery lakes following spawning in the lake. In most instances the extent of this fertilization is not known but the removal of maturing sockeye by a commercial fishery may deny lake waters of their essential nutrients and contribute to lowered productivity. Particular attention has been focussed on the imbalance of phosphate in the natural fertilization of lakes from decomposing salmon carcasses (Krokhin, 1959) and the suggestion has been made (Krokhin, 1967) that a positive balance should be maintained by the artificial replacement of the phosphate with inorganic fertilizers.

Early studies carried out in a small unstratified lake in Alaska (Nelson and Edmondson, 1955; Nelson, 1958) showed that the addition of phosphate and nitrate fertilizer resulted in increased length and weight of sockeye smolts leaving the lake. The potential role of a natural imbalance of phosphate in nursery lakes on sockeye salmon is emphasized in the following quotation from Foerster (1968):

> One wonders whether sufficient significance has been given to this feature of the phosphate balance. With sockeye populations in all areas showing such evident declines, despite legislation on regulation and limitation of fishing, it might well be that some basic factor such as this may be having a much more limiting effect on productivity than seems apparent. In addition to the smaller amounts of phosphorus introduced into a lake in the carcasses of fewer sockeye spawners, there may also be occurring a steady decline in the phosphate content of the runoff waters as the phosphates of the soil and rock become leached out over the years. Future studies of the phosphate balance of sockeye-producing waters and the direction of its trend may prove most enlightening. Addition of suitable fertilizers may be found advantageous.

In recent years it has become more evident that suitable fertilizers should not only include phosphates but also other nutrients, including trace elements, in order to increase aquatic productivity (Goldman, 1960, 1964).

The theory and application of adding natural fertilizers to aquatic environments has been practiced in fish farming for many centuries. Parsons et al. (in press; 1972) have presented data on various aspects of lake fertilization studies carried out by others. In summary of these findings, there is much evidence to show that the larger the sockeye smolts at the time of seaward migration, the higher the percentage return from the sea (Burgner, 1962; Ricker, 1962). Since food supply is one of the important factors

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governing growth, the effect of increasing the food supply to underyearling sockeye salmon through artificial fertilization of Great Central Lake, B.C., is presented here. It has already been established (Parsons et al., in press; 1972) that the waters of Great Central Lake are relatively unproductive of sockeye salmon, the average size of yearling smolts at the time of seaward migration being much smaller than in Babine Lake, B.C. (63 mm versus 79 mm) (McDonald, 1969). The average size of yearling smolts from 14 other lakes in Washington, British Columbia, Alaska, and Kamchatka is larger than the yearling smolts from Great Central Lake (Foerster, 1968). In the following account particular attention is given to changes in size of juvenile sockeye salmon in Great Central Lake associated with changes in their food supply prior to and after the addition of inorganic nutrients (see Parsons et al., 1972; LeBrasseur and Kennedy, 1972).

STUDY AREA

Great Central Lake (Figure 1) is located in central Vancouver Island, British Columbia. The lake is about 33 km long and varies between 1 and 2.5 km in width. The shoreline length is 72 km and the surface area is ca. 51 km^2. Elevation of the lake surface is 83 m above sea level and the mean depth is 200 m, with a maximum depth of about 280 m. The outlet of the lake runs into the Stamp River. Most of the shoreline slopes very abruptly into deep water. This feature is an important factor in regulating horizontal distribution of juvenile salmon in the lake, by providing a maximum amount of the lake surface available to juvenile sockeye.

LAKE SPAWNING

A brief account of the spawning sites of the sockeye salmon is presented here because the location of the in-lake spawning grounds is an important factor in the emergence of the alevin and dispersal of the fry at the time of their initial intake of food. Little or no published information is available on the migration and spawning of adults in the lake. Mr. F. C. Boyd of the Department of the Environment has kindly granted permission to refer to his internal manuscript reports on the subject.

Adult sockeye salmon bound for Great Central Lake first enter the Stamp River as early as the first week in June. This migration up the Stamp River continues through June, peaks in July, and in most years, ends in early August. The peak

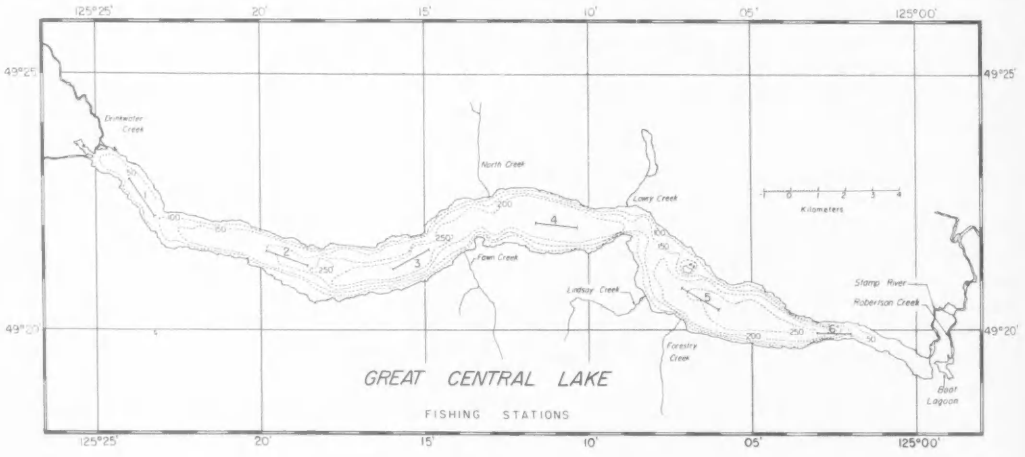

FIGURE 1.—Great Central Lake showing the six fishing stations and depth contours in meters.

of migration may not occur until the first week in September. It takes between 2 and 5 days for the sockeye to migrate up the Stamp River into Great Central Lake, depending on the water levels in the river. The fish remain in the lake but do not commence to spawn until the latter part of September. Great Central Lake is one of the few lakes in British Columbia where most of the spawning occurs in areas along the lakeshore rather than in tributary streams. Only a few hundred sockeye spawn in tributary streams a short distance away from the lake. Drinkwater, Lindsay, and Fawn Creeks (Figure 1) receive most of the stream spawners.

Lakeshore spawning commences in the last week of September, reaches a series of peaks in three principal locations during October, and ends in November. About 50% of the spawning occurs along 4.63 km of lakeshore between Lindsay Creek and Forestry Creek, 30% along 1.1 km of shoreline west of Fawn Point, and 20% along 1.6 to 4.8 km of lakeshore off North Creek. Redds were found at depths between 0.6 and 24 m but most were between 12 to 15 m. Spawnings were observed by scuba divers at depths as great as 41 m. It is now realized that the location of separate major in-lake spawning areas is important in providing the potential basis for the immediate and rapid distribution of juvenile sockeye throughout the lake, shortly after the fry emerge from the gravel and commence to feed. Two spawning areas are adjacent to the lake area where fertilizer was applied (see Parsons et al., 1972).

METHODS

LOCATION AND DISTRIBUTION OF JUVENILE SOCKEYE SALMON

A high frequency (200 kHz) moist paper recording echo sounder (Furuno model No. FNV-3000)[2] was used to locate the young sockeye in the lake and monitor their horizontal and vertical distribution. During the day, young sockeye are generally distributed throughout the lake at depths between 45 and 90 m, but are most abundant at about 65 m. They commence to migrate toward the surface about half an hour before sunset. In the summer months at civil twilight, when the sun is 96° from the zenith (or 6° below the horizon) they are distributed irregularly in density between 5 and 30 m. At nautical twilight when the sun is 102° from the zenith (or 12° below the horizon) the juvenile sockeye form a layer between the depths of 10 and 20 m, with a maximum density of about 14 m. At night during the winter months they are distributed more uniformly between 20 and 60 m. In summer the downward migration commences shortly before sunrise and is usually complete 15 to 30 min after sunrise.

The young sockeye were sampled with midwater trawls. Sampling commenced at night when the fish were in a layer between 10 and 20 m. Samples were also collected during daylight at different depths throughout the depth range of the young sockeye. The depth of trawling was adjusted to coincide with the depth of maximum fish concentration as shown by the echo sounder traces.

FISHING GEAR

A trawl net with a mouth opening 3 m wide, 6.1 m deep, and 17.7 m long was towed at 2.7 to 3.2 km/hr by a single vessel, the *Decibar*, to sample the sockeye between the depths 5 and 25 m. Three mesh sizes of knotless nylon netting were used in the construction of the net: 5 cm and 2.5 cm stretched mesh in the body and 1.3 cm in the cod end. The cod end measured 1.2 m wide by 1.8 m deep at the mouth and it tapered to a blunt end about 76 cm in diameter. A standard Henson plankton net (350μ mesh) 76 cm in diameter at the mouth, was secured to the blunt aft end of the cod end to retain the smallest juvenile sockeye and minimize the loss

[2] Reference to trade names in the publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

of their minute scales by abrasion against netting in the main cod end of the trawl.

An Isaacs-Kidd midwater trawl was towed from the *Decibar* to sample the juvenile sockeye at depths greater than 25 m and to evaluate the fishing capabilities of the large midwater trawl towed at the same depths. The mouth opening of this trawl was 1.9 m^2 and the net was constructed of 6.3 mm stretched mesh knotless netting.

FISHING STATIONS

Juvenile sockeye were sampled with trawls taken at intervals of about 3 weeks at 6 different stations (Figure 1). Most of the tows were of 30 min duration but some tows were shorter, when the echo sounder traces indicated that young sockeye were especially abundant between 12 and 14 m at night.

ANALYSES OF SAMPLES

The length of all fish was measured to the nearest millimeter from the snout to the end of the central rays of the caudal fin. This measurement is referred to as the fork length. Lengths of smaller fish were measured in a graduate tray under a binocular microscope; calipers were used for larger individuals.

All fish were weighed by fork length groups using a center-loading milligram balance (KERN Model No. T1226-1). Weights recorded are from "blot-dried" specimens. Moisture was blotted from the exterior of the fish, and gentle pressure was applied to the buccal cavity and branchial chamber to remove moisture from these spaces. Age was determined from scales using $\times 254$ projections of thermoplastic impressions.

Stomach analyses for food were done on fish selected to represent proportionally as complete a size range as possible. The food weight was measured by subtracting weight of stomach shell from weight of stomach plus food. The number of all species of food organisms were counted according to size and state of condition of each stomach examined.

RESULTS

FOOD OF UNDERYEARLING (AGE 0) SOCKEYE

During the latter part of March and up to mid-April, 1970, pre-mature fry[3] (24 to 28 mm fork length) with a small portion of the yolk sac remaining were caught at night at a depth of 14 m in midlake positions off the 3 major spawning areas. A few fry (28-30 mm) with empty stomachs were caught during the day at depths between 35 and 100 m in late March, and the first actively feeding fry (28 to 33 mm) were caught at depths between 12 and 55 m at night during the latter part of April. The number of fry caught at midwater depths increased in May at Stations 3, 4, 5, and 6 and reached a maximum in June at all stations. Fry continued to be caught in July and were still being caught in trawl nets at night in late August and early September. The fry and larger underyearling sockeye ate the same food organisms throughout the year, but the larger juvenile fish had more food in their stomachs.

Figure 2 shows the number and weight of all species of food organisms per underyearling sockeye (Age 0) from August, 1969, when inlake sampling began to April, 1970, when about 85% of the fish migrating were yearling smolts.[4] The percentage of the total number of the six major food categories from all the fish sampled for stomach contents through the same period is shown in Figure 3. A list of the different genera of food organisms found in the stomachs of juvenile sockeye from 1969 to 1971 is given in Table 1; the smallest is listed at the top of the column and the largest at the bottom.

Epischura was the predominant form (60%) in the stomachs in August, 1969 but was almost replaced by *Holopedium* (60-80%) from September to December (Figure 3). The incidence of

[3] "Embryo" is defined as a larva minus its yolk-sac. An "alevin" is a larva of an age following hatching but prior to yolk absorption. Following this stage the fish becomes a "fry" (cf. Bams, 1969).

[4] In 1969 ca. 86% of migrant smolts were yearling, 10% were 2 year old, and 4% were 3 year old. In 1970 ca. 85% of smolts were yearling and 15% were 2 year old.

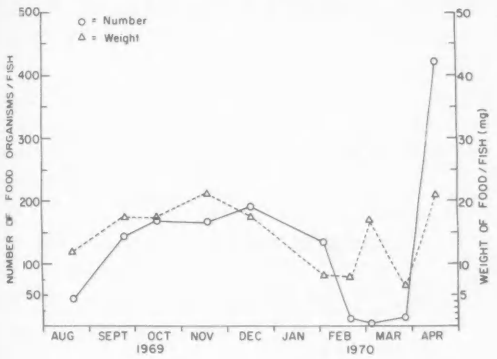

FIGURE 2.—Average number and weight of all food organisms (all species combined) per fish for underyearling sockeye salmon in Great Central Lake from August, 1969 to April, 1970.

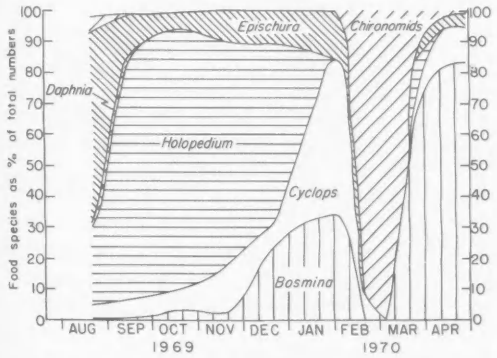

FIGURE 3.—Food of underyearling sockeye salmon expressed as a percentage of the total number of organisms from August, 1969 to April, 1970.

TABLE 1.—List of organisms found in juvenile sockeye stomachs.

Size range	Organism
mm	
0.3-0.6	*Bosmina*, usually *B. coregoni*
0.6-1.1	*Cyclops*, usually *C. biscuspidatus thomasi* and *C. vernalis*
0.9-1.2	*Holopedium gibberum*
0.9-1.5	*Daphnia*, usually *D. longiremis*
0.8-1.3	*Diaptomus*, usually *D. oregonensis*
2.0-2.5	*D. kenai*
1.1-1.9	*Epischura nevadensis*
3	Insects of the order Diptera (other than Chironomidae)
3-5	Insects of the family Chironomidae—larvae
8-11	Insects of the family Chironomidae—larvae
6-11	Larvae of the sculpin, *Cottus asper*

Bosmina and *Cyclops* increased gradually from less than 5% in August to a peak of 30 to 50% in January-February, 1970. Chironomid larvae were the only organisms eaten from February to early March and in turn were replaced by *Bosmina* (80%) in late March and April. The percentages of *Epischura* and *Holopedium* in the stomachs by number (Figure 3) and by weight (Figure 4) were similar from August to December. There was a pronounced difference between the percentages by number and by weight of *Cyclops* and *Bosmina* per fish. Although the percentage by numbers of both organisms per fish increased markedly between December, 1969 and February, 1970, the percentage weight per fish remained less than 7% for *Bosmina* and never exceeded 20% for *Cyclops*. The importance of the chironomid larvae in the diet of underyearling sockeye from February through March to early April, 1970 is more indicative when expressed as a percentage by weight (Figure 4) than by number of organisms (Figure 3).

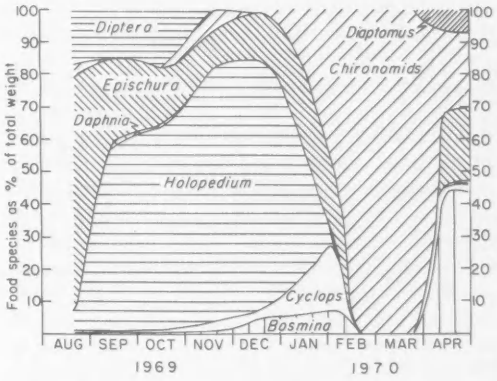

FIGURE 4.—Food of underyearling sockeye salmon expressed as a percentage of the total weight of organisms from August, 1969 to April, 1970.

The fry which emerged in late March and April, 1970 commenced to feed actively by mid-April and, as juvenile sockeye, they continued to increase their intake in number and weight of all food organisms throughout the summer,

reaching a peak in September-October (Figure 5). In August, 1970, 3 months after lake fertilization began, the underyearling sockeye had twice the number of organisms per stomach as in August, 1969 and contained about 60% more food by weight. The high consumption in September-October, 1970 represents an increase of about 45% in number of organisms, and 40% by weight, compared to the stomach contents per fish in the same period in 1969. A slight decline in number and a significant decline in weight of food organisms per fish was shown from November, 1970 to February, 1971; an abrupt increase occurred to a second high in March, which represented an increase manyfold over March, 1970. This increased food consumption occurred 1 to 2 months prior to their emigration from the lake as yearling smolts.

Five species of food organisms contributed chiefly to the diet of underyearling sockeye in Great Central Lake in 1970. In April and May *Bosmina* contributed about 50% of both the total number (Figure 6) and total weight (Figure 7) of all organisms found in their stomachs. The numbers of *Bosmina* consumed were insignificant throughout the rest of 1970 and the first 3 months of 1971. *Epischura* was the most important food organism from May to July (Figures 6 and 7) and was probably the principal source of energy for the rapid growth of the underyearlings during this period (see Figures 11 and 12). There was a transition in late July and August when *Cyclops, Holopedium,* and *Daphnia* gradually became more abundant in the stomach samples. In the 3 months which followed, September to November, *Cyclops* and *Holopedium* were the predominant genera. *Cyclops* continued in importance and formed about 50% of the number of food organisms to the end of January, 1971. However, during this period of 6 months *Cyclops* formed only 15 to 30% of the food by weight whereas *Holopedium* constituted 30 to 80% by weight. *Diaptomus* was first observed in the stomachs in the latter part of October, increased markedly in December and January, and was the predominant food organism by number in February and March, 1971. Thus *Diaptomus* was the most numerous food organism in the stomach samples just before

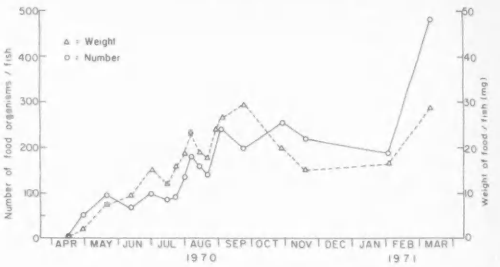
Δ = Weight
o = Number
Number of food organisms / fish
Weight of food / fish (mg)
APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR
1970
1971

FIGURE 5.—Number and weight of all food organisms per fish, for underyearling sockeye salmon from April, 1970 to March, 1971.

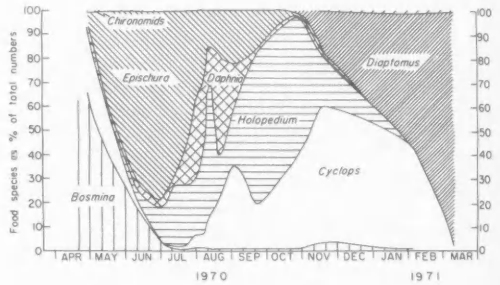

FIGURE 6.—Food of underyearling sockeye salmon expressed as a percentage of the total number of organisms from April, 1970 to March, 1971.

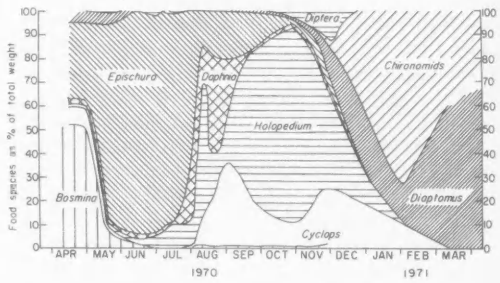

FIGURE 7.—Food of underyearling sockeye salmon expressed as a percentage of the total weight, from April, 1969 to March, 1971.

smolt migration in 1971. *Bosmina* was the most numerous in the previous year. The few chironomid larvae (Figure 6) in the diet of juvenile sockeye from December, 1970 to March, 1971, formed 30 to 70% by weight of all the food organisms (Figure 7). The importance of chironomid larvae during the winter months was observed also in the previous winter (Figures 3 and 4).

FOOD OF YEARLING (AGE 1) SOCKEYE

Those underyearling sockeye in Great Central Lake in 1969 which did not migrate to sea as yearling smolts in 1970, but remained in the lake for a second year, attained a mean length of only 51 mm and weight of 1.1 g between the latter part of April and May, 1970, whereas the migrating smolts had a mean length of 70 mm and weighed 3.5 g. The yearling sockeye which remained in the lake were collected from samples taken at all six stations and not from the end of the lake where smolts were schooling and heading seaward. Reference will be made later to the fact that the smallest size smolt, caught in the Robertson Creek weir (Figure 1) or in the nets set to capture smolts in the Stamp River, measured 55 mm and weighed 1.5 g.

Food organisms found in the stomachs of the yearling sockeye were similar to those eaten by the underyearlings during most of the year in 1970, but the yearling sockeye were more selective in cropping the larger forms of zooplankton (Figure 9). Both the underyearling and yearling sockeye fed heavily upon *Epischura* from May to July (Figures 6 and 9), but it was evident from the large numbers and weight of food organisms per fish (Figure 8) that the yearling sockeye elected to feed or were able to prey more heavily upon *Epischura* (Figure 9) than the underyearlings during September and October. Few yearling sockeye were caught in the trawls during the winter months of 1970-1971 prior to their migration as 2-year-old smolts. *Diaptomus*, *Holopedium*, and *Cyclops* were in the stomachs of these fish.

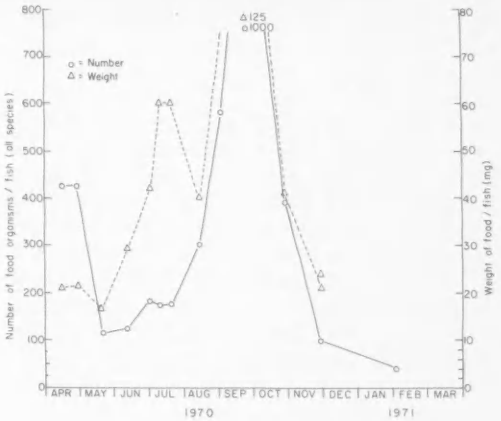
Number of food organisms / fish (all species)
Weight of food / fish (mg)
○ = Number
△ = Weight
△125
○1000
APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR
1970
1971

FIGURE 8.—Number and weight of food organisms of yearling sockeye salmon from April, 1970 to February, 1971.

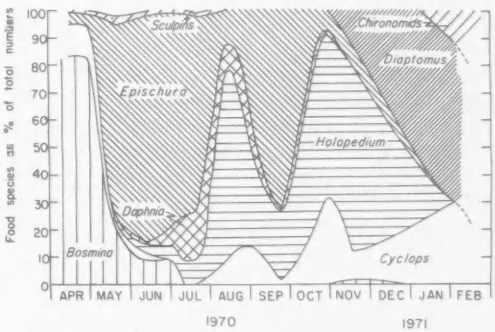

FIGURE 9.—Food of yearling sockeye salmon expressed as a percentage of the total number of organisms from April, 1970 to February, 1971.

DIEL FEEDING OF JUVENILE SOCKEYE

From midafternoon on June 17 to midday on June 18 a series of 11 tows, each of 15 min duration, were made with an Isaacs-Kidd midwater trawl. The trawl was towed through the middle of the densest portion of the stock during their

diel migration. The tows were made to determine what portion of different food organisms contributed to the salmon's ration during the day and night, as well as during the period of their diel migration. Data on depth and time of each tow, the number, size range, and mean length of sockeye caught, together with those sampled for the number and species of food organisms, and the weight of the food as a percentage of the body weight are given in Table 2.

The degree of freshness of food organisms was arbitrarily determined as fresh, fragmented, or largely unidentifiable. Fresh food was designated when no indication of digestion had occurred. The percentage of fresh zooplankton in the stomachs is given in Table 2. Depth of the densest portion of the layer of juvenile sockeye at different times of the day and night is indicated in Figure 10a by a broken line. The depth and time of each trawl tow relative to the depth of the fish is also indicated in Figure 10a.

The 24-hr data collection shows that in the day the densest portion of the layer of juvenile sockeye was formed at 75 m where the temperature of the water was 4° C; of the fish examined for stomach contents (Table 2) from tow No. 1, few food organisms per fish (Figure 10b) were noted and only 5% of the species were in fresh condition (*Bosmina*). The remaining species, *Epischura*, *Cyclops*, and *Daphnia*, were digested. Tow No. 2, through a less dense secondary layer at 105 m, indicated the same feeding pattern. Young sockeye commenced to migrate upward from 75 m between 1700 and 1800 hr. No differentiation in migration between underyearling or yearling sockeye could be detected at any level in the layer, either by net sampling or from high frequency echograms.

A tow just after sunset at a depth of 35 m revealed that the fish were eating *Bosmina* and *Cyclops* (Figure 10c) as they moved upward and 22% of the contents were in fresh condition. At 2200 hr the sockeye had passed 25 m where the heaviest concentration of *Cyclops* and *Daphnia* was located (LeBrasseur and Kennedy, 1972); in passing they had eaten *Cyclops* (Figure10c). It should be recognized, however, that there is a natural time lag between feeding at any depth and the time the fish was captured by the trawl at a shallower depth, as they migrated toward the surface.

At nautical twilight, most of the fish had completed their upward migration and were distributed in a layer between 10 and 20 m where temperatures ranged from 6° to 12°C (Figure 10a). Echograms indicated many of the juvenile sockeye salmon appeared to spend brief periods between 0 and 10 m at temperatures ranging from 14° to 23° C, during which time the young fish fed heavily upon *Epischura* (Figure 10c). In the 4 hr between the beginning and end of nautical twilight no feeding occurred (Table 2).

TABLE 2.—Diel feeding of juvenile sockeye; tows made with an Isaacs-Kidd midwater trawl, each of 15 min duration, over a 24-hr period from June 17 to 18, 1970 at Station 4 in Great Central Lake.

Tow No.	Depth of tow	Time (PST) at start of 15 min	Number fish caught	Size range underyearling	Mean length	Mean weight	Size range sampled for food	Mean length	No. sample for food	Total no. food organisms	No. of organisms per fish	% fresh	Weight of food as % body weight
	(m)			mm	mm	mg	mm	mm					
1	75	1449	47	23-40	32	292	28-40	33	10	190	19	5.5	1.1
2	105	1538	17	27-36	30	212	27-36	31	9	112	12	--	1.0
3	55	1820	21	27-38	32	272	27-38	33	10(1)[1]	67	7	--	1.0
4	35	2018	11	27-36	31	263	27-36	32	10	164	16	22	1.0
5	18	2142	6	26-36	31	282	26-36	31	6(2)	132	22	46	1.6
6	14	0023	71	26-41	32	315	26-41	33	11	537	49	6	1.7
7	19	0254	50	26-39	32	296	28-39	34	10(1)	257	26	--	1.5
8	62	0517	14	28-39	32	271	28-39	32	14(4)	586	41	64	2.1
9	68	0738	10	29-37	33	320	29-37	33	9	447	50	84	1.6
10	70	0945	9	29-39	33	278	29-39	33	9	543	60	34	1.6
11	75	1159	6	31-39	35	353	31-39	35	6	324	54	2	2.1
				Time of sunset		2011	Time of sunrise			0350			
				Time of nautical twilight		2201	Time of nautical sunrise			0200			

[1] Number in parentheses is number of items in sample which contained no food in stomachs.

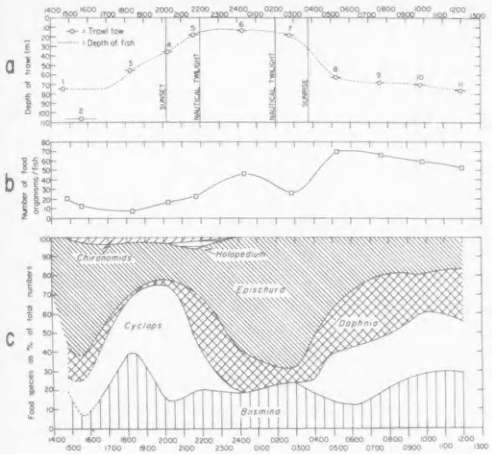

FIGURE 10.—(a) Depth of the densest portion of the layer of juvenile sockeye salmon at different times of the day and night from June 17 to June 18, 1970 is indicated by a broken line. A secondary layer is shown at 105 m for a 2-hr period. The depth of each tow with a midwater trawl is shown relative to the depth of the fish. (b) Number of all food organisms of underyearling sockeye. (c) Food species of underyearling sockeye salmon expressed as a percentage of the total number of organisms.

A second feeding period was noted at the time of the diel migration downward. Stomach samples from juvenile sockeye collected during this period contained many fresh *Daphnia* and *Cyclops* in tows 8 to 10. Only 2% of the zooplankton in the stomachs of sockeye caught at midday were in a fresh condition (Table 2), which indicates a marked reduction in feeding activity.

GROWTH OF UNDERYEARLING SOCKEYE

The average size of underyearling sockeye (Age 0) in 1969 and 1970 in Great Central Lake is shown in Figures 11 and 12. A total of 1,760 underyearling sockeye were caught in 1969 and 20,783 fish in 1970 from all six stations. A complete record of all data on which this analysis is based has been reported by Barraclough and

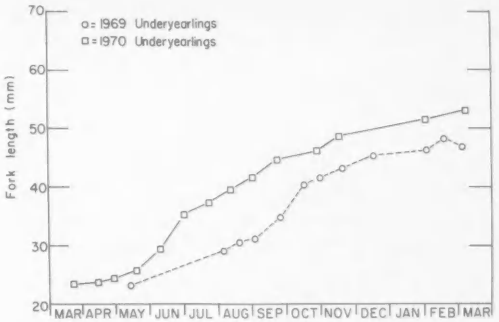

FIGURE 11.—Average length of underyearling sockeye salmon in each month, 1969 and 1970.

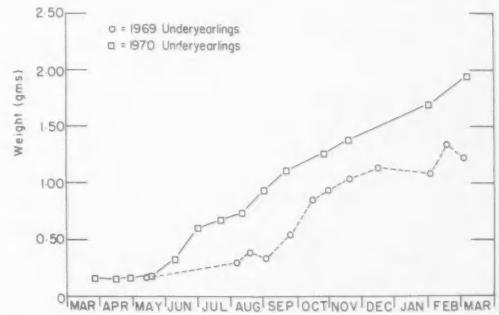

FIGURE 12.—Average weight of underyearling sockeye salmon in each month, 1969 and 1970.

Robinson (1971).[5] Although little data on the size of in-lake juveniles prior to August, 1969 are available, it is evident that a marked initial increase in length and weight of underyearlings occurred from June to July, 1970 at a time when sustained additions of nutrients were made to the lake. Growth continued steadily during the rest of 1970 and through winter months in 1970-1971.

[5] Barraclough, W. E., and D. G. Robinson. 1971. Length, weight, age and food of juvenile sockeye salmon (*Oncorhynchus nerka*) from Great Central Lake, British Columbia, May 1969 to February 1971. Fish. Res. Board Can., Manuscr. Rep. No. 1128, 268 p.

In October, 1970, when fertilization was discontinued, the underyearling sockeye salmon were about 30% heavier than the fish caught in October of 1969.

DISCUSSION

The period of freshwater growth is a very important stage in the natural production of juvenile sockeye. It is one in which mortality may be high, particularly in the very early stages of their growth. An abundant food of the optimum size readily available for the fry to prey upon is one factor which increases their survival rate (LeBrasseur et al., 1969). LeBrasseur and Kennedy (1972) determined that the biomass of zooplankton in May, 1970 before fertilization was greater than at the same time in 1969. At this time the numbers of fry caught in the midwater trawls began to increase and the catches were greatest, reaching a maximum in June at all stations shortly after fertilization commenced. LeBrasseur and Kennedy (1972) have demonstrated that the phenomenal increase in standing stocks of zooplankton in 1970 over 1969 was attributable to the sustained additions of nutrients. It is evident that the young sockeye fed very heavily (Figures 6 and 7) upon the increased number of *Epischura* in the lake (LeBrasseur and Kennedy, 1972). *Epischura* reached their greatest abundance in the upper 10 m in June when the average surface temperatures was about 15°C which was ca. 5° lower than that in July. In their diel migration, the young sockeye are able to take advantage of the most favorable temperature for food conversion for sockeye, which lies between 5° and 17°C, with a general physiological optimum at 15°C (Foerster, 1968; Brett et al., 1969). This may account for the rapid rate of growth in June compared with July.

Although the increase in length was greater in any one month in 1970 than it was in the same month in 1969, the increase in weight of about 30% in October, 1970 was less than expected from the 10-fold increase in zooplankton abundance reported by LeBrasseur and Kennedy (1972). The underyearling sockeye in the lake in 1970 were the progeny of a large escapement of 72,000 adults in 1969 and a large number of new recruits could be expected. Since most of the spawning occurred along the lakeshore it was not possible to determine the number of fry that entered the lake, particularly when it was discovered that fry were always caught in the trawls from March to August. An estimate of the total numbers of sockeye in the lake was calculated from the fish targets recorded on the high-frequency echo sounder during surveys of of the lake conducted once every 3 weeks throughout the year. From this analysis, coupled with pertinent catch data from each tow, a maximum estimate of 1×10^7 juvenile sockeye was determined. Johnson (1961) suggests that above a threshold concentration of 5,000 fish per hectare crowding may affect growth. LeBrasseur and Kennedy (1972) have demonstrated that the lake is sufficiently large that density of even a maximum estimate of 1×10^7 juvenile fish could not have been a limiting factor in their growth. However, the movement over a distance of 8 km in 1 day of large layered masses of juvenile fish in August (observed with high-frequency echo sounder) from one locality where the food source became depleted (O.D. Kennedy, personal communication) to another where food was abundant suggests that fish density may have been a seasonal factor.

The size of the yearling smolts leaving the lake from April to June each year was always larger than the same year class of juveniles caught at the six regular trawling stations during the same period because the migrating smolts school near the outlet of the lake. In 1969 the 781 yearling smolts caught in the Robertson Creek weir averaged 67.5 mm in length and 2.6 g in weight. In 1970 the average length of 1,423 yearling smolts was 71 mm and 3.5 g. In 1970 the average length of the yearling smolts decreased from 72 mm in April and May to 68 mm in June. The largest yearling smolts migrated first in April and May together with the 2- and 3-year-old smolts, and in June, almost all the smolts were smaller yearlings.

In April, 1971, 589 yearling smolts were sampled from the weir at Robertson Creek. Their average length and weight was 79 mm and 4.8 g. During this period the largest yearling smolts

ever recorded from the weir were taken, ranging from 90 to 95 mm. In May, 1971 the average length of 1,582 yearling smolts was 71 mm and a weight of 3.7 g. This average length and weight was the same as that of all yearling smolts sampled in 1970. In June, 1971, 3,012 yearlings were sampled and the smolts averaged 66 mm in length and 3.3 g in weight. It has been noted already that the smallest yearling smolt ever caught at Robertson Creek weir was 55 mm.

In conclusion, from the data presented here it is apparent that the total lake population of young sockeye salmon took advantage of the extra zooplankton ration (mainly *Epischura*) and that the average weight of individual fish of the in-lake population was 30% larger than in the previous year. However, the mechanism whereby this overall average increase in growth was observed is complex. The explanation offered is that the first fry to enter the epilimnion of the lake in April and May could take the greatest advantage of the increased zooplankton standing stock in June, when the average surface temperature was ca. 15°C. The following year (1971) this resulted in the migration of a group of 1-year-old smolts which were the largest (90-95 mm) ever observed from the lake. Fry which entered the lake in June and July could not take the same advantage of the zooplankton standing stock because the surface temperature was >16°C, and this reduced their feeding efficiency (Foerster, 1968). Thus increases in temperature of the epilimnion through the long period of fry emergence decreased the apparent benefit to late-hatching fish. However, in spite of this, most of the fry hatching later in the year achieved a length greater than 55 mm and migrated from the lake in June 1971; under normal conditions it is believed that these fry would not have reached 55 mm and would have migrated the following year as 2-year-olds. Preliminary examination of the scales from juvenile sockeye in 1971 reveals an absence of a winter check on many scales which suggests that the high concentrations of zooplankton persisting through the winter enabled many fish to smoltify and leave the lake. The combination of an early run of very large 1-year-old smolts, combined with this later run of much smaller smolts, tended to reduce the overall apparent effectiveness of lake fertilization. Thus the real effects of fertilization seem likely to be greater than would be judged from considering only changes in overall mean size of smolts.

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ESCAPE BEHAVIOR OF THE HAWAIIAN SPINNER PORPOISE (*Stenella* cf. *S. longirostris*)

WILLIAM F. PERRIN AND JOHN R. HUNTER[1]

ABSTRACT

Incidental mortality of porpoise (Cetacea, Delphinidae) occurs in the tropical tuna seine fishery. Experiments were carried out in a crowding chamber to determine behavioral responses of trained and naive Hawaiian spinner porpoise (*Stenella* cf. *S. longirostris*) to barriers of purse-seine netting, monofilament webbing, polyvinyl sheeting, rows of floats, and openings of various dimensions in a net wall. The object of the experiments was to generate information to be used in development of rescue gear and methods for the fishery. Openings of less than 1.5 m in width and/or 1 m in depth markedly inhibited escape. Negative effect of a line of floats across an opening at the surface was pronounced. Barriers of visually and acoustically relatively transparent monofilament webbing and polyvinyl sheeting were not apparently detected by porpoise prior to physical contact. Recommendations pertaining to potential design of rescue gear are presented.

Incidental mortality of porpoise occurs in the American purse-seine fishery for tropical tunas (Perrin, 1970). In 1970, the National Marine Fisheries Service began a program of research to develop improved gear and methods to reduce the porpoise mortality due to tuna seining. This paper reports the results of experiments on the responses to netting and other barriers by the Hawaiian spinner porpoise (*Stenella* cf. *S. longirostris*), a form closely related to one of the species involved in the tuna fishery.[2] We studied the response of the spinner porpoise to barriers of net, transparent monofilament nylon webbing, transparent polyvinyl sheeting, rows of floats, and to openings of different dimensions in a net wall. The results of these studies will be applied in the design of an escape opening in the tuna purse seine. The experiments were carried out at Oceanic Institute, Oahu, Hawaii, in May, June, and July 1970.

METHODS AND MATERIALS

THE ANIMALS

Three of the five porpoise (Table 1) used in the experiments had been in captivity at Oceanic Institute and Sea Life Park for various lengths of time and are referred to below as the "trained porpoise"; the remaining two, referred to below

TABLE 1.—Hawaiian spinner porpoise (*Stenella* cf. *S. longirostris*) used in behavioral experiments.

Name	Date of capture	Sex	Weight at time of capture
			kg
Trained porpoise			
Waimea	Mar. 6, 1969	Male	50.0
Nani	Dec. 4, 1969	Female	59.2
Nohea	Dec. 4, 1969	Male	65.9
Naive porpoise			
Westward	June 11, 1970	Female	72.7
Moana	July 9, 1970	Female	51.3

[1] National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA 92037.

[2] Taxonomic note: The spinner porpoise of Hawaii has been variously referred to *Stenella longirostris* Gray 1828, by Nishiwaki (1967) and Tomich (1970), and to *S. roseiventris* Wagner 1846, by Fraser (in Morris and Mowbray, 1966) and Rice and Scheffer (1968). The spinner porpoise of the tuna grounds of the far eastern Pacific has been referred to *S. microps* Gray 1846 (Miller and Kellogg, 1955; Handley, in Hester, Hunter, and Whitney, 1963; Nishiwaki, 1967; Pilson and Waller, 1970) and to *S. longirostris* (Rice and Scheffer, 1968; Harrison, Boice, and Brownell, 1969). No critical review of the genus has been accomplished since True's work on the Delphinidae in 1889. The usage here of *S. longirostris* for the Hawaiian spinner is provisional pending the results of taxonomic studies underway at the Southwest Fisheries Center and elsewhere.

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as the "naive porpoise," were freshly captured, were not exposed to any training procedures prior to the experiments, and were tested immediately upon arrival at the Institute.

THE APPARATUS

The crowding chamber (Figure 1) was constructed in a large pool at the Oceanic Institute. The pool, known as "Bateson's Bay," is roughly circular, 24.7 m across at its greatest diameter, and approximately 4 m deep at its center. A smaller holding tank communicates with the pool through a wooden gate. Three hemispherical underwater viewing ports allow surveillance of the entire pool.

Net barriers were placed at various points along the pool wall to construct a circular enclosure or crowding chamber about 20 m in diameter in which porpoise were tested. The crowding chamber had two radial walls of netting that extended from the outer edge of the chamber to a central aluminum mast. One of the walls was stationary and was provided with escape openings of various dimensions. The other wall was movable and was used to drive the animals through the opening in the stationary wall. The movable wall pivoted on the central mast and was supported along the leading edge by an aluminum beam and on the distal end by a plastic float. The edge of the pool was marked at 1° intervals.

The walls were made of tuna purse-seine webbing (4¼-inch stretched mesh [10.8 cm] #42 thread knotted nylon). Flotation was provided by purse-seine-type corkline constructed of 6-inch diameter × 3½-inch (15 × 9 cm) sponge-plastic floats.

The basic escape opening was 18 ft (5.5 m) wide and 6 ft (1.8 m) deep. Flaps of purse-seine webbing were laced in, to variously decrease width to 10, 5, or 2½ ft (approximately 3.0, 1.5, or 0.8 m) and/or depth to 3½, 3, 2, 1, or ½ ft (approximately 1.1, 0.9, 0.6, or 0.2 m). For tests of response to a barrier across the opening at the water surface, a corkline constructed of hollow plastic floats (5 × 9 inch [13 × 23 cm], 4 per m) was strung across the top of the opening. In tests of response to barriers of acoustically low-reflective materials, a panel of 3⅜-inch (stretched) mesh (8.6 cm) #12 monofilament webbing, a panel of 0.38-mm-thick polyvinyl sheeting, or a panel of 1.04-mm-thick polyvinyl sheeting, was laced into the opening.

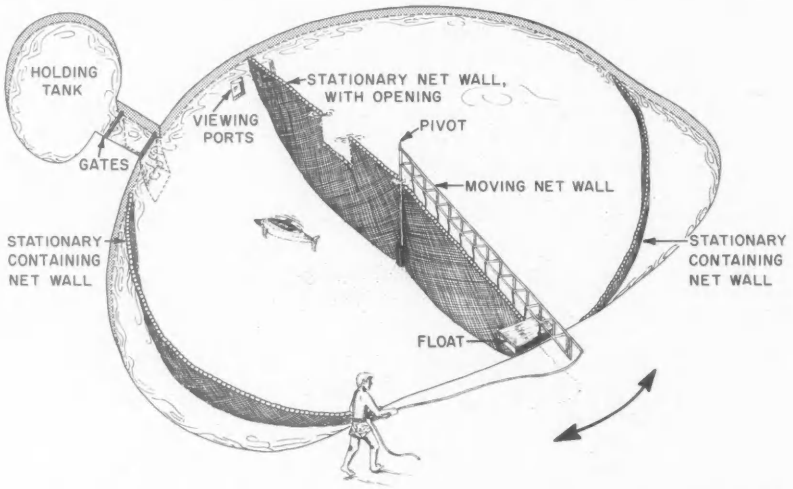


FIGURE 1.—Crowding chamber. Largest diameter of pool is 80 feet. Sketch not drawn to scale.

Acoustical tests carried out by the Naval Undersea Research and Development Center, San Diego, Calif., on plastic sheeting of similar thicknesses indicated effective acoustic transparency in the range of porpoise emanations (personal communication from W. E. Evans).

PROCEDURES

The moving wall was rotated around the center mast at a rate sufficient to completely close the chamber in about 4 min. An attempt was made to maintain a constant rate of rotation. Time required for an animal to escape from the chamber was recorded in seconds with a stopwatch, and position of the moving wall at time of escape was recorded in degrees. The reading in degrees was later used to calculate surface area remaining in the crowding chamber at time of escape. The wall was rotated alternately in clockwise and counterclockwise directions. After escape of an animal, the moving net wall was rotated until it was against the stationary wall, and the two radial nets remained together until the beginning of the next trial. Trails were spaced initially at 15-min intervals, to allow time for changing the escape opening. After our proficiency in altering the opening increased, the interval was decreased to 10 min.

Two major types of experimental design were used: (1) a long series of trials alternating two treatments and (2) a series of blocks of consecutive trials of various treatments. In some experiments, the two approaches were combined to yield a factorial design testing simultaneously the effects of variation in two or three of the factors of width, depth, and presence or absence of corkline, monofilament, or polyvinyl barriers. In some tests of the monofilament and polyvinyl panels, the animal was subjected to a single trial with the panel after a series of learning trials without the panel or at the beginning or conclusion of an experiment involving other variables. The design of these experiments is referred to below as "single trial." The results of the first series of experiments (Waimea I, II, and III; see Table 2) using the alternating trials design indicated a probable influence by the direction of rotation of the net wall or by stage of practice effect. The small number of trials in each experiment precluded complete randomization, but the treatments in subsequent experiments were staggered to offset the effect of direction of rotation. A typical sequence of trials was: *a, b, a, b, a, a, b, a, b, b;* where *a* and *b* were different treatments, and rotation in the first trial was clockwise, in the second counterclockwise, and so on in alternating fashion. In this manner, an equal number of clockwise and counterclockwise trials was assured for each treatment.

TABLE 2.—Preliminary experiments with trained porpoise.

Porpoise	Experiment	Variables tested	Design	Number of trials
Waimea	I	Width	Alternating trials	20
	II	Width	Alternating trials	20
	III	Depth, corkline	Factorial	26
	IV	Monofilament panel	Single trial	14
Nani	I	Depth	Alternating trials	20
	II: trials 1-19	Width, depth	Factorial	19
	trial 20	Corkline	Single trial	1
	III: trial 1	Corkline	Single trial	1
	trials 2-16	Depth	Block	16
	trials 17-30	Depth, monofilament panel	Factorial	14
Nohea	I	Depth	Alternating trials	22
	II	Depth	Block	36
	III: trials 1-36	Width	Block	36
	trials 37-44	Depth	Alternating trials	8
	trial 45	Monofilament panel	Single trial	1
	IV	Width, depth, corkline	Factorial	32
	V: trials 1-8	Depth	Alternating trials	8
	trial 9	Thin polyvinyl panel	Single trial	1
	VI: trials 1-8	Depth	Alternating trials	8
	trial 9	Thick polyvinyl panel	Single trial	1

The remaining surface area between the advancing net wall and the stationary wall at the time of escape was used as a criterion of the animals' readiness to escape. This index was the inverse of latency, since the smaller the area that remained when the animal escaped the longer would be the latency. Although we measured latency in seconds, we felt the net position was the preferable measurement because the rate of net movement was imprecise, whereas the actual stimulus for escape, the reduction in the swimming area, could be measured relatively accurately. In presentation of the data, the logarithm (to base 10) of the remaining area at the time of escape is plotted on trial number.

Because procedures and plans were modified during the course of the experiments, results and interpretation are combined in the presentation of the results.

PRELIMINARY EXPERIMENTS WITH TRAINED PORPOISE

We anticipated that the behavior of the porpoise would change rapidly during the course of the experiments; thus, to avoid wastage of the naiveté of the limited and expensive supply of untrained animals, we conducted a series of preliminary experiments with three trained porpoise (Table 2, Figures 2-4).

WIDTH OF OPENING

The effect of the width of the opening on the escape behavior of the three trained porpoise was first tested by presenting on alternate trials an escape route of standard width, 5.5 m, and one either 3.1 or 3.8 m wide. In Waimea (Figures 2-I and II) and Nohea (Figure 4-IV) there was some evidence that the porpoise escaped sooner when the wider escape route was used but not in Nani (Figure 3-II). We felt this was probably an artifact of experimental design as described above and consequently we considered only the data from the block experiments for evaluating effects of width on the trained porpoise. To determine the width of opening that would influence performance, Nohea was tested over six

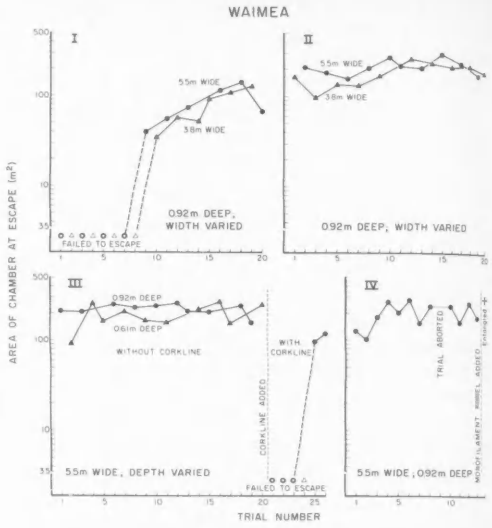


FIGURE 2.—Results of experiments with trained porpoise Waimea. Each plot summarizes one day's continuous experimentation, as follows: I. May 21, II. May 22, III. May 23, IV. May 25, 1970.

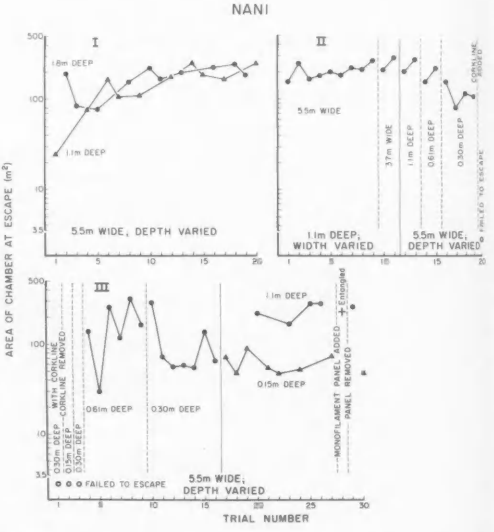


FIGURE 3.—Results of experiments with trained porpoise Nani. I. May 26, II. May 27, III. May 28, 1970.

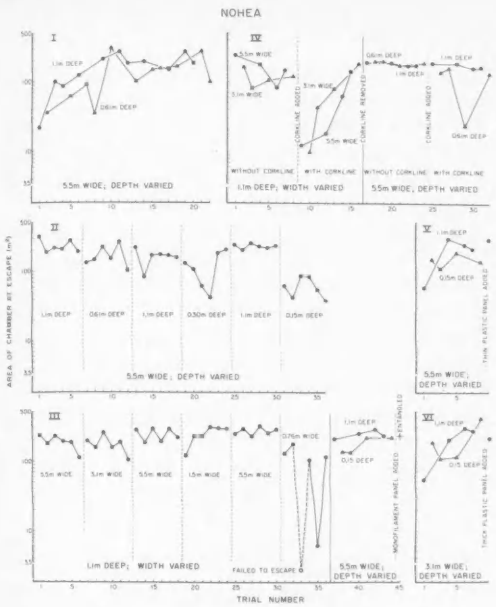


FIGURE 4.—Results of experiments with trained porpoise Nohea. I. May 30, II. May 31, III. June 1, IV. June 21, V. June 28, VI. June 29, 1970.

blocks of six trials each (Figure 4-III). The width of the escape route was 3.1 m in the second, 1.5 m in the fourth, and 0.76 m in the sixth block of experimental trials, with interspersed blocks of trials at 5.5 m. A significant decrease in performance occurred only when the escape opening was narrowed to 0.76 m. In one trial at 0.76 m the animal refused to leave the crowding chamber and had to be extricated from the webbing. In others, the porpoise exhaled air and sank passively to the bottom of the pool and did not move even when the chamber was completely closed. Exhalation of air and sinking to the bottom was a pattern that appeared in other porpoise in other experiments and was accompanied by failure to escape.

Our tentative conclusion was that the width of the opening was not a significant variable in the block experiments if it exceeded about 1.5 m.

DEPTH OF OPENING

We determined the effect of the depth of the escape route by varying depth of the hole from 1.8 m to 0.15 m while maintaining the standard hole width of 5.5 m. We will describe the results for each porpoise separately since the experiments were different for each animal.

Waimea failed in the first eight trials to escape through an opening 0.92 m deep (Figure 2-I). Performance improved thereafter to a plateau that was maintained throughout a subsequent identical experiment the next day, throughout a series of alternating trials with 0.92-m- and 0.61-m-deep openings on the third day of the experiments, and in a fourth experiment (Waimea IV) 2 days later with a 0.92-m-deep opening.

Nani showed no difference in response after the first two trials with openings 1.8 m and 1.1 m deep (Figure 3-I). High performance continued through a series of trials with a 1.1-m-deep opening, but dropped in blocks of trials of 0.61-m- and 0.30-m-deep openings (II). In subsequent experiments Nani failed to escape twice when openings 0.15 m and 0.30 m deep were used and performed erratically in blocks of trials with openings 0.61 m and 0.30 m deep (III). After seven trials with the 0.30-m opening, no failures was experienced in seven trials with a 0.15-m opening, but the animal escaped consistently earlier (larger remaining area) when the 1.1-m-deep opening was used.

Nohea escaped earlier when the hole was 1.1 m than when it was 0.61 m deep in 14 of the first 16 trials of an alternating series (Figure 4-I). In a subsequent series of blocks of trials at decreasing depths (II), a pronounced drop in performance occurred at depths of 1 ft and 5 ft. The following day's performance remained at a high level except when a corkline was strung across the opening (IV).

Our tentative interpretation of the above results was that a critical depth of opening lay near 1 m: 11 failures to escape occurred at 0.92 m or shallower; none occurred with openings 1.1 m deep or deeper; and performance was even more adversely affected by further decreasing the depth of the opening. We also concluded that the results of the first few trials for each ani-

mal were of most importance in predicting the probable response of naive wild porpoise, as the animals were able quickly to achieve high levels of performance even at very shallow depths.

CORKLINE

A corkline across the top of the opening caused Waimea (III) and Nani (II) to fail on initial trials, and greatly affected the performance of Nohea (IV). Waimea, after four failures, overcame reluctance to pass through an opening with a corkline at the surface and reachieved a high level of performance. An interaction between the corkline and depth of opening was apparent in the factorial experiment with Nohea. Initial trials with the corkline (second block) produced a temporary drop in performance with a 1.1-m-deep opening. In the fourth block, the corkline was again inserted, and performance dropped at 0.61 m depth but not at 1.1 m.

MONOFILAMENT PANEL

When the panel of nylon monofilament webbing was inserted into the opening (1.1 m deep) after a series of trials in which performance was consistently high, Waimea (IV), Nani (III), and Nohea (III) swam into the webbing as if it did not exist. Performance in subsequent trials without the panel was not affected (Nani III). Upon hitting the webbing, the porpoise became entangled and had to be extricated by a diver.

POLYVINYL PANEL

In the two single trials with a panel of clear polyvinyl sheeting inserted in the opening, Nohea (V and VI) hit the panel and slid over the top as it buckled. No difference was noted in behavior in these trials from that in trials in which the panel was absent.

During these experiments Nohea in several trials passed back and forth through the opening two or three times after the initial escape, while the net wall was being closed. The values for the surface area index shown in the figure are for the first passage. The incidence of such behavior throughout the course of all the experiments occurred only after considerable experience with a particular net configuration. In most cases, only one or two double "escapes" occurred during an experiment.

EXPERIMENTS WITH NAIVE PORPOISE

Eleven experiments were conducted with the naive porpoise (Table 3, Figures 5 and 6). The first naive animal, Westward, was captured on June 12, 1970, and after a relatively short handling period was placed in Bateson's Bay. Her swimming behavior during the first 5 days of captivity was unlike that of the trained porpoise. The trained porpoise continually swam about the tank during and between experiments, diving and "porpoising," and spinning. Westward, on

TABLE 3.—Experiments with naive porpoise.

Porpoise	Experiment	Variables tested	Design	Number of trials
Westward	I	Depth	Alternating trials	20
	II	Depth	Alternating trials	20
	III	Depth	Block	36
	IV: trials 1-40	Depth, width, corkline	Factorial	40
	trial 41	Monofilament panel	Single trial	41
	V	Width	Block	36
	VI: trials 1-10	Depth, thin polyvinyl panel	Factorial	10
	trials 11-15	Thick polyvinyl panel	Block	5
Moana	I	Depth	Alternating trials	11
	II	Depth	Alternating trials	20
	III	Width	Block	36
	IV	Depth	Block	24
	V: trials 1-12	Depth	Block	12
	trials 13-25	Width, corkline	Factorial	13

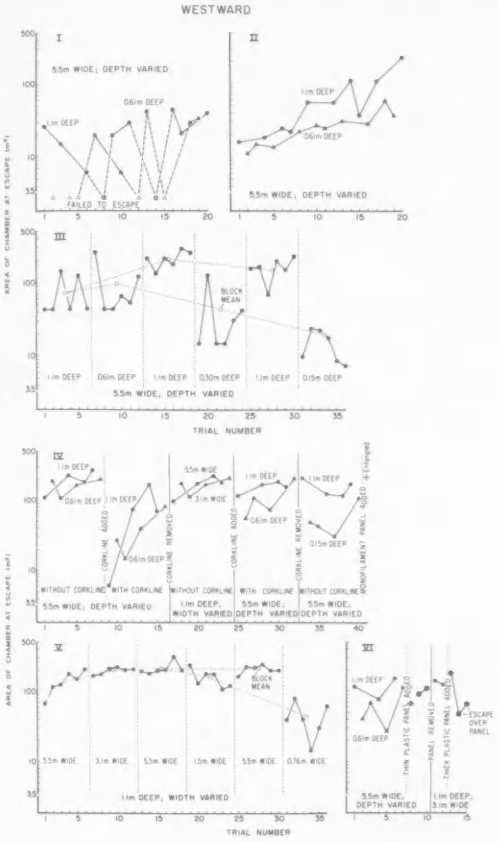


FIGURE 5.—Results of experiments with naive porpoise Westward. I. June 12, II. June 22, III. June 24, IV. June 25, V. June 26, VI. June 29, 1970.

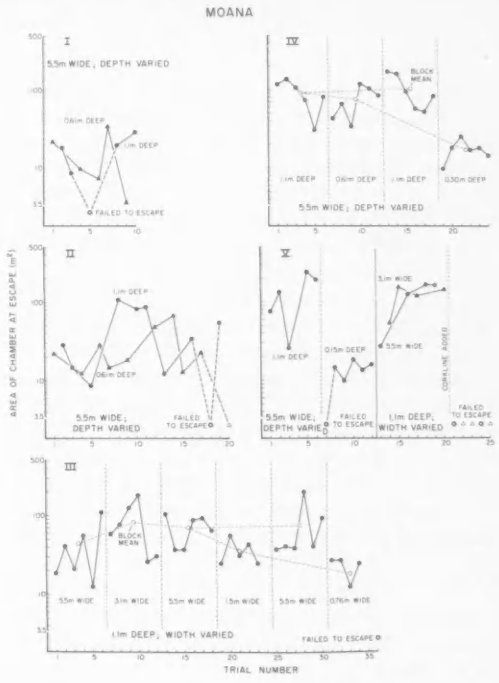


FIGURE 6.—Results of experiments with naive porpoise Moana. I. July 10, II. July 11, III. July 12, IV. July 13, V. July 15, 1970.

the other hand, remained at the surface in a near-upright position with blowhole exposed and rostrum submerged, swimming very slowly with slow, low-amplitude beats of the posterior half of the body. Her head bobbed up and down slightly as she swam. Opinion among the animal-training staff of the Oceanic Institute as to the cause of this behavior was divided; some believed the animal to be in shock, perhaps even moribund, others believed the behavior to indicate extreme fright. The first experiment was carried out the day after capture. Subsequently Westward's behavior slowly changed, until 5 days later on June 17 it was indistinguishable from that of the trained porpoise. The remainder of the Westward experiments were carried out after June 17.

Moana, the second naive porpoise, was captured on July 9, 1970. When placed in Bateson's Bay, she exhibited the same behavior as Westward, but to a lesser extent. Periods of surface swimming in a semiupright position, but without head-bobbing, were interspersed with periods of normal porpoising and diving. During the first experiment she swam slowly at the surface in the diagonal posture but during the second and subsequent experiments, her behavior was similar to that of the trained animals.

DEPTH OF OPENING

In the first few trials (Figure 5-I) a marked difference existed in the response of Westward to an opening 1.1 m deep and one 0.61 m deep. The animal swam slowly at the surface, circling or moving back and forth in the chamber. When the opening was 1.1 m deep, she moved slowly through the opening just as the moving wall closed. When the opening was 0.61 m deep, she moved past or circled slowly in front of the opening and then dove and entangled herself in the webbing of the moving wall. In the sixth trial, her behavior became more varied; she swam in tight circles beneath the surface and attempted to pass between the end of the moving wall and the periphery of the chamber before passing through the opening, after which she slapped her tail against the water surface. Behavior in subsequent trials became increasingly erratic. In trial 13 she darted through the opening rather than moving through slowly as in the previous trials. In trial 14, she tried again to squeeze past the moving wall and became lodged in the narrow opening. In trial 15, she assumed a position across the corkline of the moving wall, half in and half out of the chamber, and remained there until removed. In the remaining trials, she moved rapidly through the opening, and in the last two, she assumed a horizontal attitude similar to that usually taken by the trained porpoise and stopped bobbing her head but still kept her blowhole above the surface.

An identical experiment (II) of alternating trials was carried out 5 days later, after all traces of the slow surface-swimming and head-bobbing behavior had disappeared. Performance was consistently higher with the 1.1-m opening. The effect of depth is clearly seen in the results of a block-design experiment for Westward (III).

The second naive porpoise, Moana, a smaller and presumably younger animal than Westward, achieved a higher rate of successful passage in the first depth experiment (Figure 6-I). She failed only once, with the 1.1-m-deep opening. In the second depth experiment (II) her performance was extremely variable compared to that of Westward, and no relation between depth and success rate existed. In two trials (18 and 20) while swimming in tight circles near the apex of the chamber, she snagged her flipper in the webbing and had to be extricated. In later block-design experiments (V and IV) the effect of depth was evident as it was for Westward.

WIDTH OF OPENING

Results of block-design experiments testing the effect of width of opening for Westward (Figure 5-V) and for Moana (III) were similar to those for the trained porpoise (Nohea), but an effect was discernible at widths of 1.5 m.

As with the other experiments, performance of Westward was higher and more stable than that of Moana. Westward began to pass through the opening two or three times during a single trial. The frequency of multiple "escapes" was higher for the 5.5-m-wide opening than for the narrower openings (Table 4).

CORKLINE

Insertion of a corkline at the surface across the top of the opening sharply affected the performance of Westward (IV) and Moana (V). The performance of Moana showed the greatest effect. After a series of preparatory trials, Moana failed to pass through the opening in five straight trials with the corkline. In each trial she laid the anterior part of her body across the corkline and remained there until removed. In the block-design experiments with Westward (IV), the second block of trials with a corkline produced a smaller drop in performance than did the first, with the 0.61-m-deep opening only, demonstrating as for the trained porpoise (Nohea IV, Figure 4) an interaction between depth and presence or absence of a barrier at the surface.

TABLE 4.—Multiple escapes of Westward.

Width of opening in block of six trials	Number of double escapes	Number of triple escapes
m		
5.5	0	0
3.1	1	0
5.5	2	2
1.5	1	0
5.5	2	0
0.76	0	0

MONOFILAMENT AND POLYVINYL PANELS

When the monofilament panel was inserted into the 1.1-m-deep opening at the end of a series of depth trials, Westward (IV) "got up a full head of steam and plowed into the monofilament" (extracted from field notes of W. Wasden) and became entangled. Insertion of polyvinyl panels produced similar results in multiple trials; Westward (VI) in each trial hit the panel and slid over it and out of the chamber. There was nothing in the behavior of the porpoise to indicate that they recognized the presence of the panels.

DISCUSSION AND CONCLUSIONS

The swimming behavior of the naive porpoise Westward and, to a lesser extent, of Moana, the first few days after capture was very similar to that of porpoise (*Stenella* spp.) in tuna purse seines as observed by one of us (Perrin) off Central America. A typical "failure to escape" episode is illustrated for Moana in Figure 7. Immediately after a purse-seine net has been set, when the diameter of the encircled area is greatest (approximately 250 m), the porpoise swim about quite rapidly in small tight groups of a dozen or so individuals, the members of a group diving and surfacing together (Figure 8). As the net is hauled and the area enclosed becomes smaller, especially after the backing down operation (see Perrin, 1969), the porpoise congregate and raft near the center of the enclosure and mill very slowly, holding their bodies in a semiupright position with blowhole exposed and rostrum at or slightly below the surface (Figure 9). At this point, individual animals can be seen to leave the group and dive. When the net has been completely hauled, animals are often found with their snouts entangled in the webbing several meters below the corkline.

Although the head bobbing exhibited by Westward was not observed in the purse-seine situation, the similarities in behavior between freshly captured animals and those captured in a purse seine were striking. In both cases the animals did not display normal motor patterns; they rested or swam at abnormally slow speeds, and this behavior was often ended by a rapid dive beneath the surface with no noticeable change in behavior preceding the act. The principal characteristics of this behavior, the inhibition of activity in a fear-inducing environment, resembled fear responses described for many other vertebrates and frequently classified as an immobility or freezing response (Ratner and Thompson, 1960; Hinde, 1970). Hogan (1965, 1966) suggested that withdrawal and immobility are separate, mutually inhibitory systems. If this view is correct, then driving porpoise through an escape route in the purse seine would not be successful once the animals began to show the immobility response, because withdrawal would be inhibited. Under these circumstances the additional fear stimulus associated with driving might be the catalyst for the rapid dive to escape, which results in entanglement. Driving may have to be carried out before immobility begins. Once the animals became immobile the only strategy may be to pull the net out from beneath them as is currently done during the "backing down operation" (Perrin, 1969).

That the behavior of Westward and Moana evolved into more typical behavior during the course of a single experiment also supports the notion that their unusual behavior was caused by the circumstance of captivity rather than ill health.

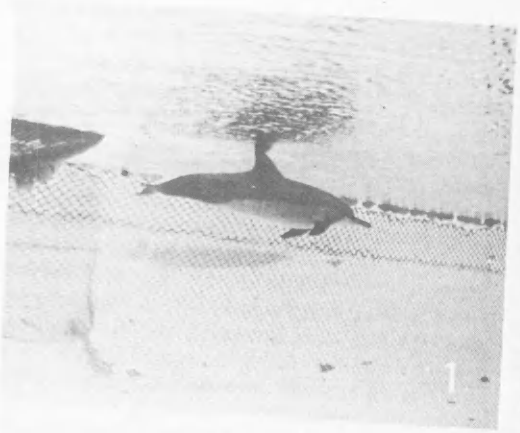
Our conclusions with respect to projected design of a rescue gate for removing porpoise from a purse seine during fishing operations were:

1. The gate should be sufficiently wide so that when the perimeter of the net circle buckles after pursing, the width does not become less than 1.5 m. Considering the equivocal results of the experiments for openings wider than 1.5 m, the opening should be as wide as practically possible.

2. Depth of the opening should be not less than 1 m and as deep as it is possible to make it without causing loss of the fish in the net.

3. There should be no line, corkline, or other barrier across the opening at the surface.

4. A self-actuating release port that will open when struck by a porpoise swimming into it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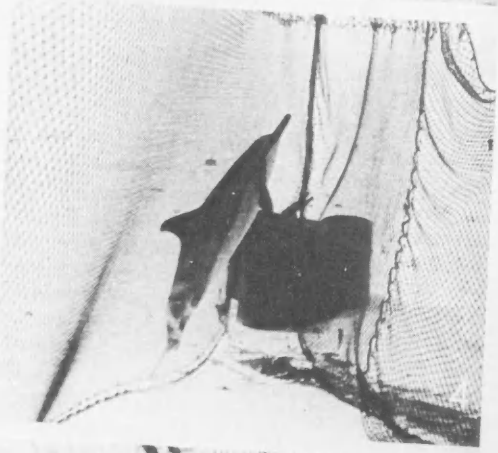

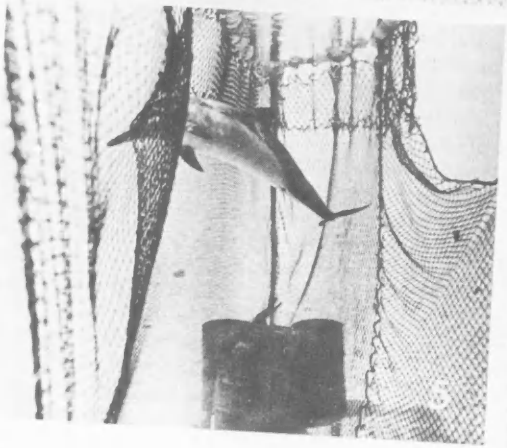

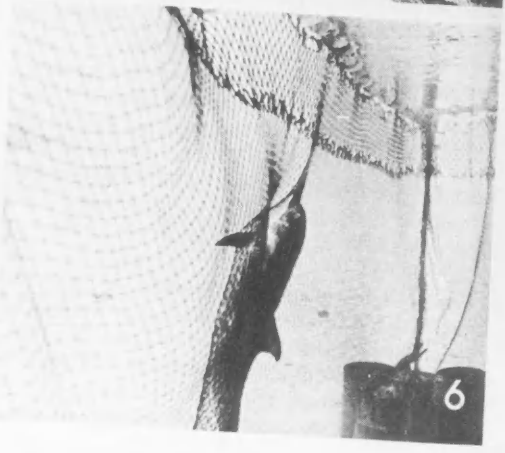
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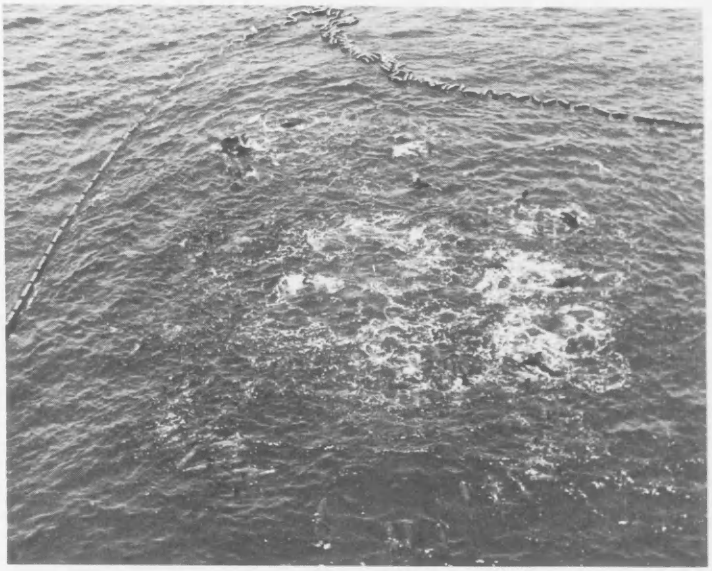
FIGURE 7.—Typical "failure to escape" episode. Moana (1) patrols moving wall at beginning of trial, then (2) takes up position at apex of chamber and remains there for most of trial, in vertical attitude. As chamber nears closure Moana dives (3), orients toward opening (4), and turns and swims into moving wall (5), becoming entangled (6).



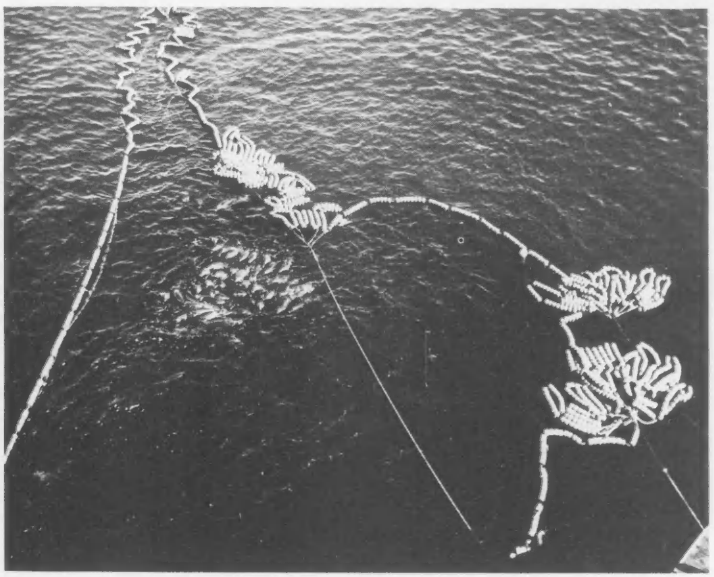


FIGURE 8.—Porpoise (*Stenella graffmani*) in tuna purse seine at beginning of set, when net is at near-maximum diameter. Animals are circling and diving in groups of a dozen or so individuals.

FIGURE 9.—Porpoise in purse seine, after most of net has been taken aboard. Animals are "rafting" in compact group, each maintaining approximately vertical attitude, with blowhole exposed and dorsal fin submerged. Large fish underwater in foreground are yellowfin tuna.

might be feasible if constructed of acoustically transparent materials, providing that it were so constructed that the fish in the net would not also use it.

5. It is to be expected that great difficulty will be encountered in inducing wild porpoise to pass through an opening in the perimeter of a purse-seine enclosure.

ACKNOWLEDGMENTS

We thank the Oceanic Institute and its Director, Dr. Kenneth Norris, for providing the facilities and the porpoise used in this study. William Wasden, National Marine Fisheries Service, Honolulu, Hawaii, assisted in all phases of the study, and porpoise trainers Ingrid Kang, Sea Life Park, and Scott Rutherford, Oceanic Institute, provided assistance and advice during the course of the experiments.

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METHODS FOR TAGGING SMALL CETACEANS

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ABSTRACT

Four types of tags have been used on four species of delphinids. These include a circular plastic button tag that is attached to the dorsal fin by a nylon bolt, a highly visible dart-type spaghetti tag that is placed near the base of the dorsal fin, a radio transmitter tag, and a freeze brand.

Use of button tags has been discontinued due to high shedding rate. The dart-type spaghetti tag has proved best for tagging large numbers of animals without capturing them. The radio tag provides very detailed information on behavior and movements, while freeze branding provides a permanent mark, though both require capturing the animal.

The importance of marking commercially valuable species of whales (primarily the larger baleen whales and the sperm whale) has long been recognized. Since their development in the mid-1920's, "Discovery-type" tags have been used to mark large numbers of these animals (Rayner, 1940; Brown, 1962; Clark 1962). Returns from these tags have provided valuable information on the species' distribution, migration, and abundance and on such basic aspects of their biology as relative growth rates and the timing of the events in their lives (Mackintosh, 1965).

The relationship of several small delphinid species to commercial fish populations and the potential of these cetaceans as a major economic resource has renewed interest in their stocks during the last decade (Perrin, 1970). Early attempts to study these populations in the wild have been hampered by the difficulty of positively identifying an animal or a population from one encounter to the next. Therefore, development of a reasonable method for marking these animals for identification would facilitate studies of their life histories.

Although several investigators have tried tagging small cetaceans, only three have had even moderate success. In a program conducted by the Oceanic Institute, Oahu, Hawaii, plastic cattle eartags were placed on two *Steno bredanensis* and one *Stenella attenuata* (Evans, 1967). This program was continued by Norris and Pryor (1970), and at least one of the tags was still on a *Stenella attenuata* when it was resighted after 3½ years.

Sergeant and Brodie (1969) tagged 812 belugas, *Delphinapterus leucas*, in Hudson Bay, Canada, over a 2-year period. Six hundred and ninety-four of these animals were tagged with a spaghetti tag originally designed by Mather (1963) for use in tagging pelagic fishes and manufactured by Floy Tag Company,[4] Seattle, Wash. The remaining 118 belugas were tagged with Petersen disc tags, similar to the button tags we used. Of the 812 animals tagged, 2 with spaghetti tags were recovered by the beluga fishery. A third spaghetti tag was observed in a live animal temporarily stranded by the ebbing tide 1 year after the original tagging.

Perrin and Orange (1971) tagged 218 *Stenella* spp. in 1969 and approximately 1,000 in 1970 in the eastern tropical Pacific with spaghetti-type dart tags. Five tags have been recovered; maximum time at liberty was 138 days (916 km net movement).

Since 1968, personnel of the Naval Undersea Research and Development Center's Marine Bioscience Division at San Diego, Calif., have been

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[4] Reference to commercial products does not imply endorsement by the National Marine Fisheries Service.

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investigating the distribution and biology of several odontocete cetaceans off the southern California coast. In order to delineate migration routes and to keep track of local herds of the common dolphin, *Delphinus delphis* auctt., a tagging program was initiated. During the same period, a tagging program was also initiated for *Tursiops truncatus* on the west coast of Florida. The special problems associated with tagging odontocete cetaceans required the modification of old and the development of new tagging techniques.

This paper discusses the relative merits of the four marking methods used by our laboratory. In addition, it presents some preliminary results of the program in order to substantiate the utility of the various methods.

METHODS AND RESULTS

We have used modified dart-type vinyl spaghetti tags (Floy Manufacturing Company) on four species of Eastern Pacific delphinids in an area from Point Conception, Calif., to Cabo San Lucas, Baja California, Mexico, and throughout the Gulf of California. Our original spaghetti tags were 5 mm in diameter by 17 cm long. In order to increase visibility and flow characteristics of the tag, we increased the length to 30 cm (Figure 1). Using the modified tag, we have marked 240 *D. delphis*, 10 *Lagenorhynchus obliquidens*, 8 *Tursiops gilli* auctt., and 13 *Stenella graffmani* to date (July 1971). The animals were all tagged at the anterior insertion of the dorsal fin while they were surfing on the bow pressure wave. Several dolphins were observed to continue riding the bow pressure wave after being tagged, so the tagging process apparently did not affect their normal behavior.

A *T. gilli* auctt., tagged on 27 October 1970, off Magdalena Bay, Baja California, was recovered by an American tuna boat off Manzainillo, Mexico, on 22 January 1971. The animal had covered at least 816 km between the time of tagging and the time of capture, a period of just less than 3 months.

Three *D. delphis* bearing spaghetti tags have been observed swimming in the vicinity of the Coronado Islands near San Diego, Calif., and at least one spaghetti-tagged *D. delphis* has been sighted off Magdalena Bay, Baja California. Each of these animals was known to have been carrying the tag for from 2 weeks to several months.

Circular plastic "button" tags (10 cm diam) (Figure 2) were through-bolted to the dorsal fins of 46 *D. delphis* and 6 *L. obliquidens* between 1967 and 1970. These tags are similar to those employed by Norris and Pryor (1970) in Hawaii, but are larger to make them more easily spotted. Button tags were attached to animals captured off the southern California coast, or near Cedros

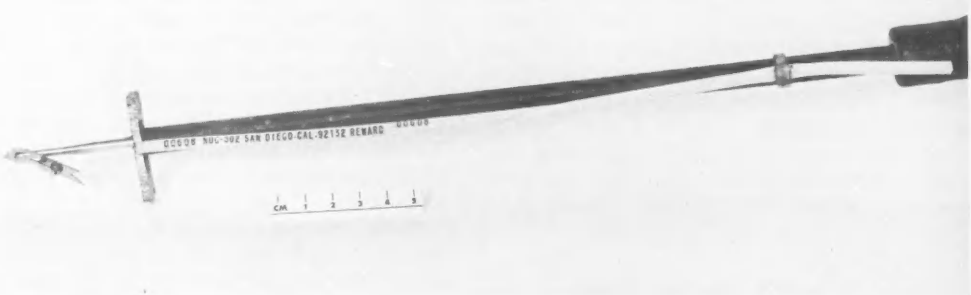

FIGURE 1.—The dart-type spaghetti tag in place on the tagging apparatus.

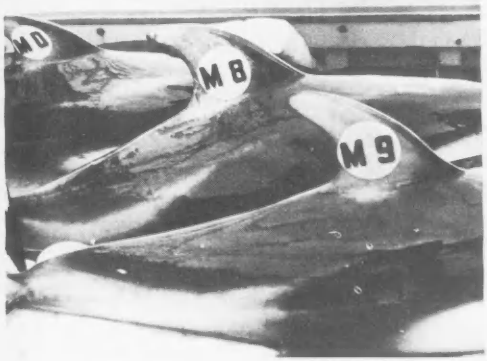

FIGURE 2.—Three *Lagenorhynchus obliquidens* with the plastic button tag, just prior to release.

Island, Baja California. Two of the *L. obliquidens* tagged in 1969 were resighted almost 1 year later, and a *D. delphis* tagged in 1968 was resighted 21 months later.

Twenty-four *T. truncatus* were tagged with the button tags near Sarasota, Fla., from August 1970 through September 1971. Animals bearing tags have been resighted several times.

The third and most successful short-term tag is the radio transmitter tag with which at least four species of small cetaceans have been successfully marked to date (Evans, in press, Martin, Evans, and Bowers, 1971). The original package used in these studies was a 27 mHz (11 m) transmitter and antenna housed in a waterproof envelope which is attached to the dorsal fin of a dolphin or a small whale by means of a spring-loaded corrosible link. The link dissolves and releases in 30 days, allowing the package to slip off the animal.

These early radio beacons, designed for short-term transmission (30-60 days), weighed up to 900 g, and though they proved especially useful in studying the detailed movements of *D. delphis* in the waters off San Diego, Calif., their size, cost, and relatively short transmission time made them unacceptable for long-term monitoring of herd movements.

To meet this need, a new lightweight radio tag (170 g) with a 9-12 month transmitter life was developed. This tag combines the advantages of a radio beacon and a button tag in that it continues to serve as a color coded marked even after it no longer transmits (Figure 3). Furthermore, the new radio tag is available commercially at less than 10% of the cost of the 900/gm transmitters.

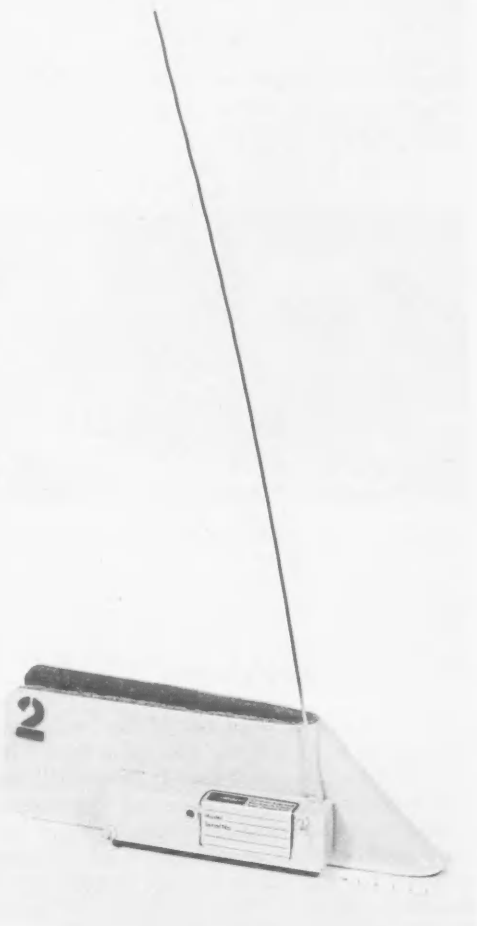

FIGURE 3.—The lightweight (170 g) radio tag.

The fourth method, freeze branding, consists of applying a supercooled branding iron, usually copper, to the epidermal surface of the dolphin for 5-30 sec. Evidence from freeze branding cattle indicates that the branding process is painless to the animal and has no lasting effect other than leaving a permanent mark (Farrell, Laisner, and Russell, 1969). Though evidence of the branding usually becomes indistinct shortly after application, after about 2 months the animal will display a highly legible brand (Figure 4). We have used this method on eight wild *T. truncatus* near Sarasota in conjunction with either a button tag or a spaghetti tag. The number on a freeze branded animal was clearly visible, from a distance of 40 yards, when the animal was resighted 10 weeks after tagging.

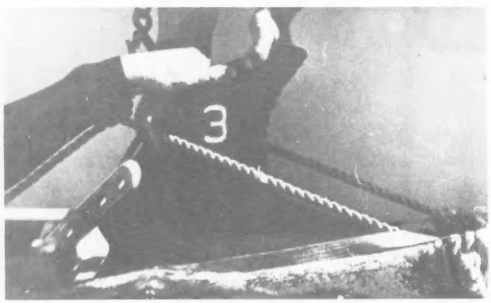

FIGURE 4.—A *Tursiops truncatus* with the freeze brand on the dorsal fin.

DISCUSSION

We have discontinued use of the button tag in favor of the spaghetti and radio tags. Incidence of loss of button tags from animals has been exceptionally high among the *T. truncatus* around Sarasota, and the few resightings of button-tagged dolphins off southern California lead us to believe that button tag loss is high in this area also. A major disadvantage of the button tag is that the animal must be captured in order to be tagged. The spaghetti tag, on the other hand, is normally placed in the animal while it is free swimming and thus does not require capture. Using this method we have placed over 50 spaghetti tags in one herd of *D. delphis* in less than 2 hr. When spaghetti tags are placed in the fibrous tissue at the insertion of the dorsal fin, incidence of tag loss appears to be lower for spaghetti tags than for the button tags (Nishiwaki, Nakajima, and Tobayama, 1966). In either case, the numbered information on the tag is so small that it cannot be read on a moving animal at sea. Unless the spaghetti tags are color-coded, resighting at sea can give no information on the original tagging location. Spaghetti tags may also be placed in an animal that has been captured.

The radio tags can be placed only on captured animals but provide very detailed information concerning exact movement and diving patterns of the animal.

While freeze branding involves capture of the animal, it appears to provide permanent and highly legible identification of cetaceans. Tomilin (1962) reported taking a Black Sea *D. delphis* in 1953 which bore a brand posterior to the eye. The brand was quite legible and contained numbered information. The source and nature of the brand were not known. In the future, we plan to freeze brand all the dolphins we capture for radio tagging and to continue to use the spaghetti tags for free-swimming delphinids.

An advertisement was placed in the July issue of *National Fisherman* requesting that any information on sightings of tagged delphinids in the Eastern Pacific be forwarded to the Marine Bioscience Division of the Naval Undersea R & D Center, San Diego, Calif. (Evans, Leatherwood, and Hall, 1971). Copies of this advertisement have been placed at sportfish landings and commercial docks from Santa Barbara to San Diego, Calif.

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A REVIEW OF THE LANTERNFISH GENUS *Taaningichthys* (FAMILY MYCTOPHIDAE) WITH THE DESCRIPTION OF A NEW SPECIES

BRENT DAVY[1]

ABSTRACT

The genus *Taaningichthys* includes three known species, one of which is here described as new.

The species of the genus *Taaningichthys* do not appear to perform daily vertical migrations. Evidence indicates vertical stratification of juveniles and adults.

Although photophores and lateral line are reduced, the species of *Taaningichthys* possess very large eyes which may be related to capture of luminescent prey.

Otoliths of all three species have been examined and found to be taxonomically important.

Bolin (1959) erected the genus *Taaningichthys* to include two species, *T. bathyphilus* and *T. minimus*, previously placed in the genus *Lampadena* by Tåning (1928). The main characters which distinguish *Taaningichthys* from *Lampadena* are: (1) the origin of the dorsal fin in *Taaningichthys* is clearly behind the base of the pelvic fins; (2) the development in *Taaningichthys* of a crescent of white tissue[2] on the posterior half of the iris, although a similar white (luminous?) crescent is present on the dorsal portion of the iris in *Lampadena chavesi* (Nafpaktitis and Paxton, 1968); (3) the presence of a single SAO, or none, in *Taaningichthys* (always three SAO in *Lampadena*); (4) reduced dentition and lateral line in *Taaningichthys*.

Taaningichthys may be distinguished from all other myctophid genera by the combination of the white crescent of tissue on the posterior half of the iris, the undivided luminescent caudal glands, and the single or altogether absent SAO.

Berry and Perkins (1966) reported what they thought to be a third form of *Taaningichthys* apparently without photophores. Following the capture of a number of specimens of this form by the RV *Velero IV* of the University of Southern California and the examination of considerable material made available to me by numerous institutions around the world, I felt that a review of the genus was appropriate.

MATERIALS AND METHODS

Members of the genus *Taaningichthys* are deep-dwelling, fragile myctophids, easily damaged by the net. Scales are readily lost, and damage to the bones of the snout, upper jaw, and operculum is very common. Consequently, measurement of jaw, head, and snout length is often very difficult if at all possible. The following measurements were taken on the best preserved specimens: Eye diameter (ED)—horizontal distance across the orbit; jaw length (JL)—length of premaxillary; predorsal (Pre D)—anterior tip of premaxillary to base of anteriormost ray of dorsal fin; preventral (Pre V)—anterior tip of premaxillary to base of anteriormost ray of ventral fin; preanal (Pre A)—anterior tip of premaxillary to base of anteriormost ray of anal fin; prepectoral (Pre P)—anterior tip of premaxillary to base of anteriormost ray of pectoral fin; preadipose (Pre Ad)—anterior tip of premaxillary to posterior end of base of adipose fin; length of supra- and infracaudal luminous glands—length of exposed luminous tissue only; anal-infracaudal distance—anterior tip of

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[2] This tissue is not visible until some time after preservation and is hardly distinguishable in specimens initially frozen and then preserved.

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infracaudal gland to end of base of anal fin. Sizes of specimens are given in standard lengths (SL) only.

Terminology of body photophores follows that of Bolin (1939). Unless otherwise specified, the term photophore refers to the primary body photophore.

Otoliths were measured with an eyepiece micrometer as follows: Length (OL)—the greatest length parallel to the sulcus; height (OH)—greatest height perpendicular to the sulcus. Following measurements, otoliths were lightly smeared with graphite to bring out detail and then photographed. Otolith terminology follows that of Frizzell and Dante (1965).

Female specimens were considered gravid when eggs included oil globules and completely filled the oviduct.

Most specimens examined were captured with open nets and depth sampled is here considered as the maximum depth reached by the net (appendix).

Counts of procurrent caudal rays are given as dorsal + ventral.

KEY TO THE SPECIES OF THE GENUS *Taaningichthys*

1a. VO 8-10; AO 5-7 + 4-6, total 9-13; Pol directly below or anterior to base of adipose fin; Prc_1-Prc_2 interspace equal to or greater than two photophore diameters; as many as five pairs of broad-based, hooklike teeth on dentary near symphysis ..... *T. minimus* (Tåning, 1928)

1b. VO, if present, 3-5; AO, if present, 1-4 + 1-2, total 2-5; Pol, if present, clearly behind base of adipose fin; Prc_1-Prc_2, if present, interspace equal to, or less than, one photophore diameter; no broad-based, hooklike teeth on dentary near symphysis 2

2a. Photophores present as in 1b above; anal-infracaudal distance half as long as length of infracaudal gland, or longer ..... *T. bathyphilus* (Tåning, 1928)

2b. Photophores absent; anal-infracaudal distance less than half length of infracaudal gland ..... *T. paurolychnus* n. sp.

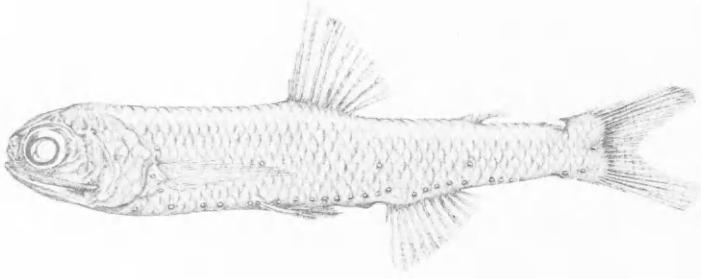

FIGURE 1.—*Taaningichthys minimus* (Tåning); 46 mm, Ocean Acre stn. 7-21.

GENUS *Taaningichthys* Bolin

Taaningichthys minimus (Tåning, 1928)

Figures 1 and 2

Lampadena minima Tåning, 1928: 63; Parr, 1928: 154, Figure 37.

Lampadena (*Lampadena*) *minima* Fraser-Brunner, 1949: 1078, Figure.

Taaningichthys minimus Bolin, 1959: 26.

D 11-13; A 12-13 (11-14); P 15-17; V 8; gill rakers 4-5+1+11 (10-13), total 16-17 (15-18); VO 8-10; AO 5-7+4-6, total 9-13; Prc 2+1; vertebrae 40-41; procurrent caudal rays 8-10+8.

Mouth terminal, moderately large, JL about 1.5 in Pre P; maxillary slightly expanded posteriorly. Eye large, ED 2.2-3.4 in Pre P. Pterotic spine long and directed posteriorly. Opercular margin concave posterodorsally, slightly convex posteriorly. Pectoral fin long, reaching VO_6 or VO_7; its base about midway between ventral body margin and horizontal septum. Pre V 2-2.4 in SL. Pre D 1.9-2.3 in SL; end of base of dorsal fin clearly in advance of vent. Pre A 1.4-1.6 in SL. Anterior end of base of adipose fin on vertical through posterior end of base of anal fin; Pre Ad 1.2-1.3 in SL.

A band of dark pigment along anteroventral margin of orbit containing a series of light gray, triangular patches of tissue not present in the other two species.

Dn absent; Vn present between anterior margin of orbit and posteroventral margin of nasal rosette. PVO_1 on or behind vertical through upper end of base of pectoral fin and about midway between it and ventral margin of body; PVO_2 in front of middle of base of pectoral fin; a straight line through PVO_1 and PVO_2 passing in front of PLO. PLO about halfway between upper end of base of pectoral fin and horizontal septum. Five PO. VLO above base of pelvic fin, usually closer to horizontal septum than to ventral margin of body. Last VO usually slightly elevated. SAO 1-2 photophore diameters below horizontal septum, directly above vent. AO level. AO series overlaps anterior end of infracaudal gland. Pol directly below or in advance of base of adipose fin, 1-2 photophore

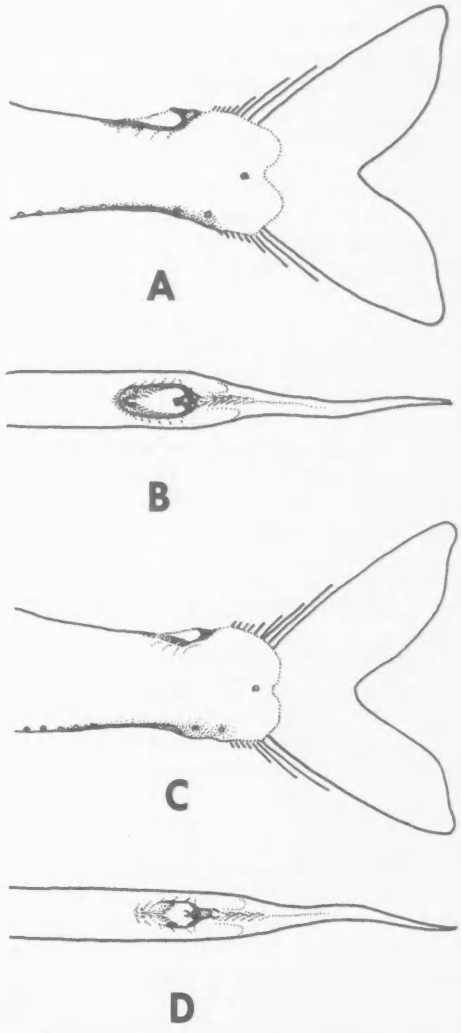

FIGURE 2.—*Taaningichthys minimus*. A. Side view, sexually dimorphic supracaudal gland of male, 53 mm. B. Top view, sexually dimorphic supracaudal gland of same male. C. Side view, sexually dimorphic supracaudal gland of female, 54 mm. D. Top view, sexually dimorphic supracaudal gland of same female.

diameters below horizontal septum. Prc_1 and Prc_2 level, behind infracaudal gland; Prc_3 at horizontal septum.

Caudal luminous glands undivided, the infracaudal larger than the supracaudal and both covered by scales. Sexual dimorphism is evident in supracaudal gland of adults (specimens about 40 mm and larger); in males this gland is about twice as large as in females (Figure 2).

Mesopterygoid teeth in narrow oval patches. Narrow band of needlelike teeth on palatine. No vomerine teeth. Both jaws with needlelike teeth which bend medially. A single row of broad-based, anteriorly hooked teeth occupying posterior two-thirds of medial surface of dentary. As many as five pairs of similar teeth, most often directed posteriorly, on medial surface of dentary near symphysis, and another two to three pairs projecting forward and laterally on symphysial area of premaxillary; below these, on anterior part of premaxillary, several posteriorly curved teeth (longer than rest of premaxillary teeth).

Taaningichthys minimus is the shallowest dwelling, most firm-bodied, and smallest of the three species, the largest examined specimen measuring 65 mm.

Gravid females (about 40 mm and larger) were captured in August-September.

Horizontal distribution—*T. minimus* occurs circumglobally between about lat 35° N and 30° S (Figure 5). It has been taken less frequently than *T. bathyphilus*.

Vertical distribution—Closing-net data from the Project "Ocean Acre" in the north Atlantic Ocean suggest vertical stratification of juveniles and adults. Juveniles appear to inhabit depths of 140 to 250 m, the smallest specimen (21 mm) having been captured at 140 m. Adults occur predominantly in depths between 450 and 500 m. *T. minimus* does not appear to perform daily vertical migrations.

Taaningichthys bathyphilus (Tåning, 1928)

Figure 3

Lampadena bathyphila Tåning, 1928: 63; Parr, 1928: 151, Figure 36.

Lampadena (*Lampadena*) *bathyphila* Fraser-Brunner, 1949: 1078, Figure.

Taaningichthys bathyphilus Bolin, 1959: 26, Figure 6.

D 12-13 (11-14); A 13 (12-14); P 12-14; V 8; gill rakers 3+1+7-8 (5-9), total 11-12 (9-13); VO 4 (3-5); AO 3 (1-4) +1(2), total 4(2-5); Prc 2+1; vertebrae 34-36; procurrent caudal rays 7+6.

Mouth terminal, moderately large, JL about 1.5 in Pre P; maxillary slightly expanded posteriorly. Eye large, ED about 2.5 in Pre P. Pterotic spine inconspicuous. Opercular margin as in *T. minimus*. Pectoral rays reaching VO_1; base of pectoral fin nearer to horizontal septum than to ventral margin of body. Pre V 2.1-2.5 in SL. Pre D 1.9-2.2 in SL; end of base of dorsal fin on, or slightly in advance of, vertical through SAO. Pre A 1.5-1.7 in SL. Base of adipose fin above end of base of anal fin; Pre Ad 1.2-1.4 in SL.

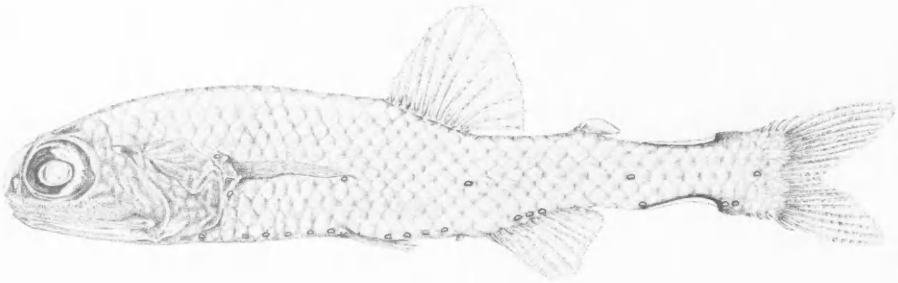

FIGURE 3.—*Taaningichthys bathyphilus* (Tåning); 62 mm, RV *Velero* stn. 11733, LACM 30034-1.

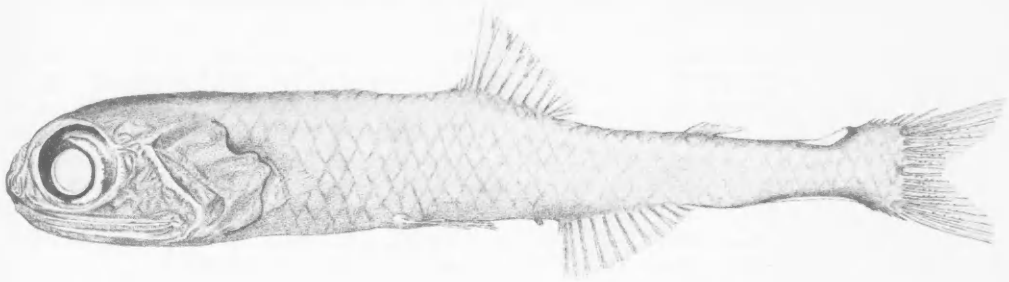

FIGURE 4.—*Taaningichthys paurolychnus*, new species, holotype, 67 mm, SIO 70-19.

Dn absent; a very small oval Vn, visible in young individuals and masked by darkly pigmented tissue in adults. Position of PVO_1 farther forward than in *T. minimus*, a line through PVO_1 and PVO_2 passing behind PLO; PVO_1 midway between upper end of base of pectoral fin and ventral margin of body; PVO_2 midway between PVO_1 and upper end of base of pectoral fin. PLO varying in position, usually closer to horizontal septum than upper end of base of pectoral fin. PO 5-6. VLO above base of pelvic fins, closer to horizontal septum than ventral margin of body. VO level. SAO 1-2 photophore diameters below horizontal septum, directly above or slightly behind urogenital papilla. AO level; AOp over anterior end of infracaudal gland. Pol position variable, generally midway between anterior end of infracaudal gland and end of base of anal fin (always well behind base of adipose fin), and one photophore diameter or less below horizontal septum. Prc_1 and Prc_2 level; Prc_3 at horizontal septum. Secondary photophores present on snout and rays of caudal fin.

Length of supracaudal luminous gland 1.5-2 in length of infracaudal; sexual dimorphism not apparent; both glands undivided and surrounded by dark pigment.

Mesopterygoid teeth rather sparsely distributed. Single row of needlelike teeth on palatines. No vomerine teeth. Both jaws with needlelike teeth which bend medially (those on the anteriormost premaxillary somewhat longer). Several broad-based, anteriorly hooked teeth on posterior medial surface of dentary (not as many as in *T. minimus*). Two to three pairs of similar teeth projecting forward and laterally on symphysial area of premaxillary.

Taaningichthys bathyphilus is the intermediate of the three species in terms of depth of occurrence, photophore development and size. It does not seem to grow larger than about 80 mm.

Of the specimens examined, only one gravid female (57 mm) was found which had been captured in late June.

Horizontal distribution—*T. bathyphilus* occurs circumglobally within a broad zone between lat 41° N and 67°31′ S (Figure 5). It appears to be more common or, perhaps, more easily captured than its two congeners.

Vertical distribution—The shallowest depth of capture for *T. bathyphilus* is 580 m (a juvenile male, 32 mm). An adult female, 65-mm long, was captured at a depth of 675 m. Members of this species have not been taken above these depths. The maximum depth of occurrence is not yet known. *T. bathyphilus* does not appear to perform daily vertical migrations.

Taaningichthys paurolychnus, NEW SPECIES

Figure 4

Holotype: 1 (67 mm), 17 Dec. 1969, 31° N, 119° W, Scripps Institution of Oceanography.

Paratypes: 1 (68 mm), 22 Nov. 1969, 17° 47′ N, 25°22′ W, National Institute of Oceanography; 1 (87 mm), 13 Sept. 1968, 17° S,

86° W, Institute of Oceanology, Academy of Sciences of the USSR, Moscow; 1 (49 mm), 20 Sept. 1961, 33° N, 17° W, Museu Municipal do Funchal; 1 (57 mm), 29 Jan. 1922, 19° N, 79° W, Zoological Museum, University of Copenhagen; 2 (79-95 mm), 17 Dec. 1969, 31° N, 119° W, 2 (65-71 mm), 10 June 1967, 35° N, 123° W, Scripps Institution of Oceanography; 1 (75 mm), 17 Sept. 1966, 1° N, 81° W, 1 (80 mm), 15 Jan. 1969, 32° N, 120° W, Smithsonian Oceanographic Sorting Center; 1 (82 mm), 13 Apr. 1962, 30° N, 120° W, 1 (77 mm), 29 Mar. 1962, 35° N, 129° W, National Marine Fisheries Service.

D 12-13 (11); A 13 (11-14); P 14 (13-15); V 8; gill rakers 3-4+1+9-10 (8-11), total 13-15 (12-16); vertebrae 35-36; procurrent caudal rays 7+6-7.

Mouth terminal, moderately large, JL about 1.5 in Pre P. Eye large, ED 2.2-3.2 in Pre P. A short pterotic spine directed posterolaterally. Opercular margin slightly concave posterodorsally to a level above upper end of base of pectoral fin, slightly convex posteriorly. Pectoral rays reaching base of pelvic fins; base of pectoral fin midway between ventral margin of body and horizontal septum. Pre V 2.1-2.3 in SL. Pre D 1.9-2.1 in SL; end of base of dorsal fin in advance of origin of anal fin. Pre A 1.5-1.7 in SL. Base of adipose fin directly above, or somewhat behind end of base of anal fin; Pre Ad 1.2-1.4 in SL.

Vn apparently absent. Head and body photophores absent. Secondary photophores present on snout and interradial membranes of caudal fin.

Length of supracaudal luminous gland 1.5-2 in length of infracaudal gland; sexual dimorphism not apparent; both glands undivided and surrounded by dark pigment.

Mesopterygoid teeth rather sparsely distributed. Single row of needlelike teeth on palatine. No vomerine teeth. Both jaws with needlelike teeth which bend medially (those on the anterior part of premaxillary somewhat longer). Several broad-based, anteriorly hooked teeth on posterior medial surface of dentary as in *T. bathyphilus*. Two to three pairs of similar teeth projecting forward and laterally on symphysial area of premaxillary.

Taaningichthys paurolychnus is the largest of the three species, the longest specimen examined measuring 95 mm. It has apparently lost its

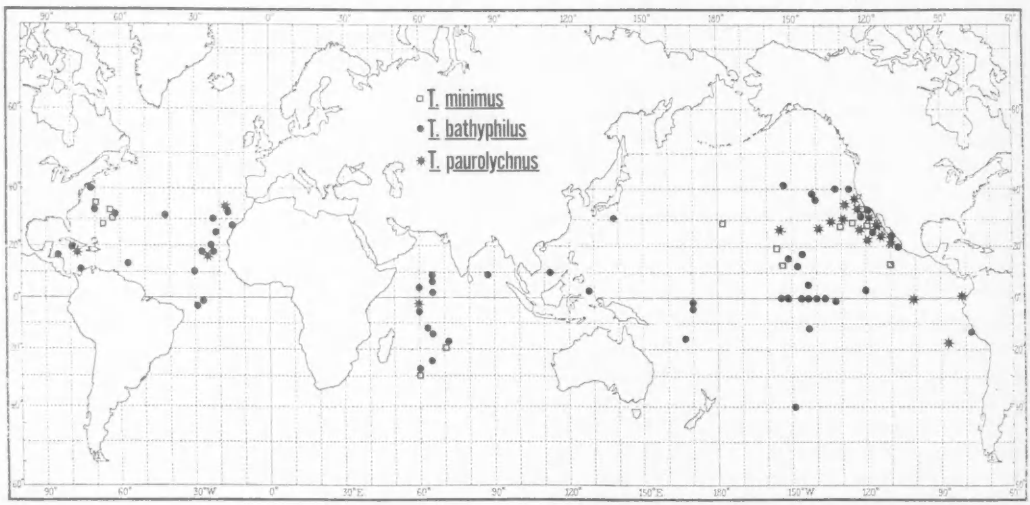

FIGURE 5.—Catch localities of *Taaningichthys minimus*, *T. bathyphilus*, and *T. paurolychnus*. Capture locality for specimen taken from 67°31′ S/90°26′ W not shown.

primary photophores, retaining only the caudal glands and the simple, presumably secondary, photophores, on the head and caudal fin. It is also the deepest dwelling of the three species.

Gravid females have been captured in March-April and August-September. The smallest gravid female examined was 65 mm.

Horizontal distribution—*T. paurolychnus* is distributed circumglobally between about lat 40° N and 20° S (Figure 5). It does not appear to be as common as *T. bathyphilus*.

Vertical distribution—*T. paurolychnus* has not been taken above 900 m (an adult female, 77 mm). The lower limits of its distribution are not yet known. *T. paurolychnus* does not appear to perform daily vertical migrations.

Etymology—The name *paurolychnus* refers to the absence of primary photophores and the presence of limited, presumably secondary photophores. It is derived from the Greek *pauros* meaning few, small, and *lychnus* meaning light.

OTOLITHS

OL as a percentage of SL ranges from 4.4 to 5.5% in *T. minimus*, 3.9 to 4.6% in *T. bathyphilus*, and 2.8 to 3.6% in *T. paurolychnus*. OH as a percentage of OL ranges from 66.7 to 77.7% in *T. minimus*, 72.1 to 77.9% in *T. bathyphilus*, and 78.3 to 91.7% in *T. paurolychnus*.

The sulcus is more pronounced in the otolith of *T. bathyphilus* than it is that of *T. paurolychnus*, but less so than in that of *T. minimus* (Figure 6). The otolith of *T. paurolychnus* has almost no antirostrum, and the antirostrum in *T. bathyphilus* is less pronounced than that in *T. minimus*. The posterior margin of the otolith in *T. paurolychnus* is nearly straight vertically, making the general outline almost square, whereas the otoliths of its two congeners are smoothly rounded posteroventrally, so that the general outline is oval. The otolith (Figure 6) of a single specimen of *T. bathyphilus* from the north Atlantic is differently shaped and very large for a specimen of its size (60 mm). However, no other differences in the fish were found and more material from the north Atlantic must be examined before anything further can be stated.

DISCUSSION

The various hypotheses and ideas regarding the function, or functions, of luminous organs of midwater fish are reviewed by Nicol (1969). The photophores within the genus *Taaningichthys* show drastic reduction in terms of numbers and development. *T. minimus* has, relatively, the best developed photophores as well as the greatest number; these organs are seldom rubbed off unless the specimen is damaged. *T. bathyphilus* has fewer and less well-developed photophores which are easily rubbed off. *T. paurolychnus* has lost all primary photophores but retains simple, presumably secondary, photophores on the snout and caudal fin. As already mentioned, there are no indications that the members of the genus *Taaningichthys* undertake diel vertical migrations as most myctophids do. It may therefore be that photophores of the myctophid type are not selected for in a deep-water, nonmigratory fish, which would account for the reduction of these organs and, eventually, their loss. Unlike photophores, eyes are very well developed in *Taaningichthys*, regardless of depth of occurrence. Even the deepest of the species has large, nearly binocular eyes. This may be correlated with the food habits of these fish. Myctophids, in general, feed on zooplankters, many, if not most, of which are bioluminescent. It is possible therefore that *Taaningichthys* strongly depends on large, presumably highly effective eyes for locating and capturing its prey, which is probably not very abundant in those dark midwater depths. Furthermore, retention of this energetically expensive visual equipment may account for the very poorly developed lateral line system.

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I thank Basil G. Nafpaktitis of the University of Southern California, Robert J. Lavenberg of the Los Angeles County Museum of Natural History, and Theodore W. Pietsch of the University of Southern California for their critical review of the manuscript and helpful suggestions. Thanks are also due to John E. Fitch

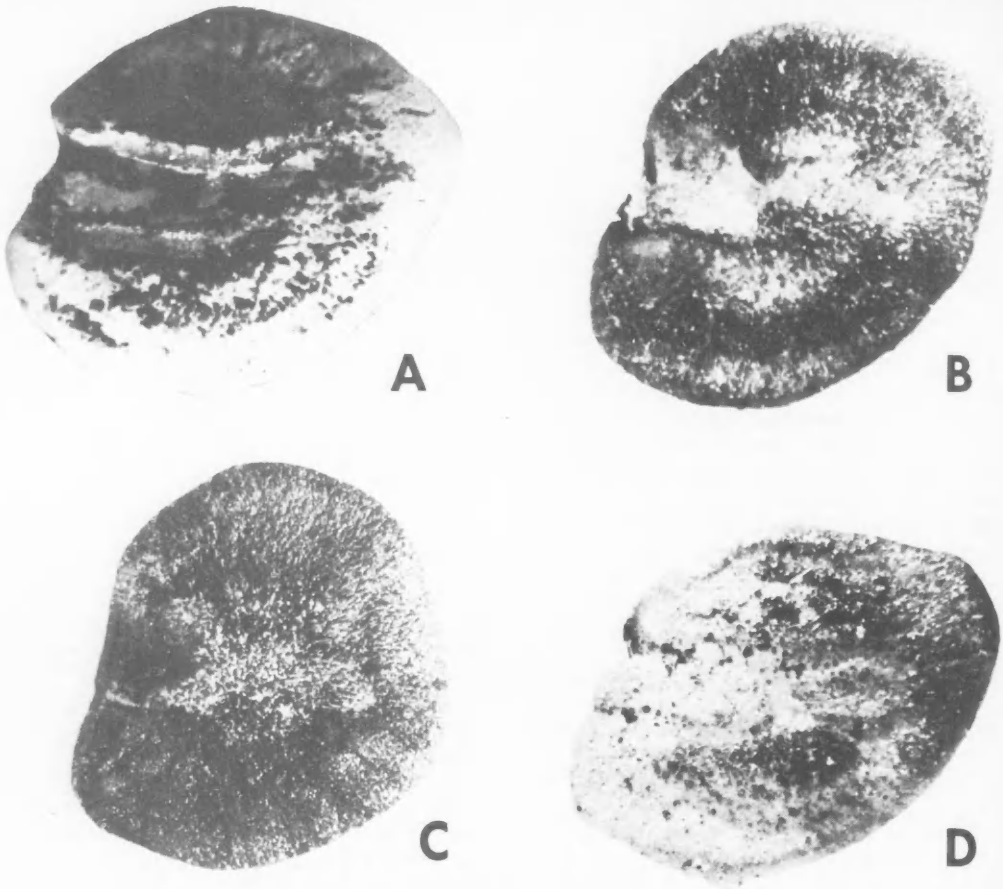

FIGURE 6.—Medial views of right otoliths, anterior end to the left.
A. *Taaningichthys minimus*, otolith 2.0 mm long, specimen 49 mm.
B. *T. bathyphilus*, otolith 1.8 mm long, specimen 64 mm.
C. *T. paurolychnus*, otolith 1.7 mm long, specimen 87 mm.
D. *T. bathyphilus*, otolith 2.3 mm long, specimen (from north Atlantic) 60 mm.

of the State of California Department of Fish and Game for comments concerning otoliths.

I am indebted to several people and their institutions for making specimens available: Robert L. Wisner, Scripps Institution of Oceanography (SIO); Julian Badcock, National Institute of Oceanography, Surrey, England; Robert J. Lavenberg; Jørgen Nielsen, Zoological Museum, University of Copenhagen; V. E. Becker, Institute of Oceanology, Academy of Sciences of the USSR, Moscow; Robert H. Gibbs, Jr., U.S. National Museum; Leslie W. Knapp, Smithsonian Oceanographic Sorting Center; G. E. Maul, Museu Municipal do Funchal, Madeira; Thomas Clarke, University of Hawaii; E. H. Ahlstrom and H. Geoffrey Moser, National Marine Fisheries Service; Richard H. Backus and James E. Craddock, Woods Hole Oceanographic Institu-

tion; G. Palmer, British Museum (Natural History); Michel Le Gand, Office de la Recherche Scientifique et Technique Outre-Mer, Nouméa, New Caledonia (material presented to the Los Angeles County Museum of Natural History).

Illustrations were made by Sharon Calloway, Los Angeles County Museum of Natural History, and otoliths were photographed by the Photography Department, Los Angeles County Museum of Natural History.

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APPENDIX

Material examined

Taaningichthys minimus

University of Southern California, RV *Velero IV*:
Stn. 11168, 31 July 1966, 32° N/120° W, 350 m, 10-ft IKMT, 1 (36 mm), LACM 9705.
Stn. 11185, 2 Aug. 1966, 29° N/118° W, 375 m, 10-ft IKMT, 1 (47 mm), LACM 9650.

International Indian Ocean Expedition, RV *Anton Bruun*, Cruise III:
Stn. 156, 6 Sept. 1963, 29° S/60° E, 122 m, 10-ft IKMT, 1 (45 mm), LACM 31320.

University of Hawaii, Institute of Marine Biology:
LACM 31574, 11 Sept. 1969, Hawaiian waters, 380 m, 6-ft IKMT, 2 (55-57 mm).
LACM 31575, 30 Oct. 1969, Hawaiian waters, 780 m, 6-ft IKMT, 2 (63-65 mm).
LACM 31576, 13 Nov. 1969, Hawaiian waters, 575 m, 10-ft IKMT, 2 (50-60 mm).

Scripps Institution of Oceanography:
SIO 57-86, 12 May 1955, 29° N/125° W, 700 m, 10-ft IKMT, 1 (42 mm).
SIO 62-430, 24 Aug. 1962, 29° N/130° W, 600 m, 10-ft IKMT, 1 (52 mm).
SIO 68-490, 22 Sept. 1968, 29° N/178° W, no depth, 10-ft IKMT, 1 (46 mm).
SIO 69-341, 27 Mar. 1969, 13° N/110° W, 1,100 m, 10-ft IKMT, 1 (42 mm).

Woods Hole Oceanographic Institution:
RHB stn. 1112, 17 June 1965, 22° N/70° W, 200 m, 10-ft IKMT, 1 (28 mm).
RHB stn. 1735, 8 July 1968, 28° N/67° W, 870 m, 10-ft IKMT, 1 (40 mm).

Zoological Institute, Academy of Sciences of the USSR, Leningrad:
RV *Vitiaz* stn. 4885, 20 Dec. 1960, 17° S/71° E, 2,700 m, RT, 1 (27 mm).
RV *Vitiaz* stn. 5127, 28 Oct. 1961, 13° N/154° W, 1,000 m, CN, 1 (48 mm).

National Marine Fisheries Service, RV *Horizon*:
Cruise H6204, stn. 100-140, 15 Apr. 1962, 28° N/124° W, 1,676 m, 10-ft IKMT, 1 (53.5 mm).
Cruise H6204, stn. 110-160, 17 Apr. 1962, 35° N/124° W, 1,676 m, 10-ft IKMT, 1 (50 mm).

U.S. National Museum, Ocean Acre material:
Stn. 2-2N, 6 Mar. 1967, 32°26′ N/63°44′ W, 140 m, 6-ft IKMT, 1 (21 mm).
Stn. 3-3N, 4 July 1967, 33°4′ N/64°37′ W, 1,060 m, 10-ft IKMT, 1 (52.5 mm).
Stn. 3-4N, 4 July 1967, 33°10′ N/64°45′ W, 480 m, 10-ft IKMT, 1 (37 mm).
Stn. 3-6N, 5 July 1967, 33°9′ N/64°33′W, 250 m, 10-ft IKMT, 3 (36-45.2 mm).
Stn. 3-13N, 6 July 1967, 32°54′ N/64°45′ W, 161 m, 10-ft IKMT, 1 (20.5 mm).
Stn. 4-9A, 4 Sept. 1967, 31°52′ N/63°58′ W, 479 m, 10-ft IKMT, 1 (49 mm).
Stn. 4-9B, 4 Sept. 1967, 31°52′ N/63°58′ W, 479 m, 10-ft IKMT, 1 (42 mm).
Stn. 4-16C, 6 Sept. 1967, 32° N/64° 17′ W, 500 m, 10-ft IKMT, 1 (41 mm).
Stn. 6-7B, 26 Apr. 1967, 31°47′ N/63°53′ W, 155 m, 10-ft IKMT, 1 (33.5 mm).

Stn. 6-15B, 28 Apr. 1967, 32°13′ N/63°51′ W, 160 m, 10-ft IKMT, 1 (33 mm).
Stn. 6-15P, 28 Apr. 1967, 32°13′ N/63°51′ W, 160 m, 10-ft IKMT, 1 (34.5 mm).
Stn. 6-18P, 29 Apr. 1967, 32°14′ N/63°46′ W, 750 m, 10-ft IKMT, 1 (30 mm).
Stn. 6-26N, 30 Apr. 1967, 32°18′ N/63°55′ W, 200 m, 10-ft IKMT, 1 (29 mm).
Stn. 7-14N, 8 Sept. 1967, 32°12′ N/63°25′ W, 250 m, 10-ft IKMT, 1 (45 mm).
Stn. 7-15N, 8 Sept. 1967, 32°21′ N/63°29′ W, 450 m, 10-ft IKMT, 1 (42 mm).

Taaningichthys bathyphilus

University of Southern California, RV *Eltanin*:
Stn. 947, 27 Jan. 1964, 67°31′ S/90°26′ W, 2,690 m, 3-m IKMT, 1 (67 mm), LACM 10424.
Stn. 1724, 18 July 1966, 40°06′ S/149°55′ W, 1,180 m, 3-m IKMT, 1 (60 mm), LACM 11247.

University of Southern California, RV *Velero IV*:
Stn. 8959, 17 Oct. 1963, 33° N/119° W, 900 m, 10-ft IKMT, 1 (69 mm), LACM 6435.
Stn. 10607, 10 June 1965, 33° N/119° W, 900 m, 10-ft IKMT, 1 (61 mm), LACM 6723.
Stn. 966, 15 May 1964, 33° N/118° W, 750 m, 10-ft IKMT, 1 (72 mm), LACM 8525.
Stn. 8238, 25 Oct. 1962, 33° N/118° W, 10-ft IKMT, 1 (64 mm), LACM 9036.
Stn. 9860, 25 June 1964, 33° N/118° W, 750 m, 10-ft IKMT, 1 (60 mm), LACM 9089.
Stn. 11538, 21 June 1967, 32° N/118° W, 1,300 m, 10-ft IKMT, 1 (66 mm), LACM 9676.
Stn. 11539, 21 June 1967, 33° N/118° W, 950 m, 10-ft IKMT, 1 (63 mm), LACM 9677.
Stn. 11617, 16 Aug. 1967, 31° N/118° W, 1,130 m, 10-ft IKMT, 1 (68 mm), LACM 9682.
Stn. 11312, 25 Jan. 1967, 28° N/116° W, 1,325 m, 10-ft IKMT, 1 (58 mm), LACM 9708.
Stn. 10373, 23 Feb. 1965, 33° N/118° W, 10-ft IKMT, 2 (61-68 mm), LACM 9764.
Stn. 11696, 12 Oct. 1967, 32° N/118° W, 860 m, 10-ft IKMT, 1 (67 mm), LACM 9796.
Stn. 11733, 8 Nov. 1967, 20° N/106° W, 1,400 m, 10-ft IKMT, 1 (62 mm), LACM 30034.
Stn. 11767, 16 Nov. 1967, 24° N/109° W, 1,500 m, 10-ft IKMT, 1 (57 mm), LACM 30045.
Stn. 12066, 12 Apr. 1968, 26° N/114° W, 1,300 m, 10-ft IKMT, 1 (61 mm), LACM 30075.
Stn. 12072, 14 Apr. 1968, 29° N/118° W, 750 m, 10-ft IKMT, 1 (65 mm), LACM 30079.
Stn. 12184, 24 July 1968, 31° N/119° W, 820 m, 10-ft IKMT, 1 (50 mm), LACM 30271.
Stn. 12597, 17 Jan. 1969, 32° N/120° W, 770 m, 10-ft IKMT, 1 (67 mm), LACM 30348.
Stn. 12392, 11 Oct. 1968, 32° N/118° W, 1,110 m, 10-ft IKMT, 1 (61 mm), LACM 30403.
Stn. 12349, 12 Sept. 1968, 32° N/118° W, 1,400 m, 10-ft IKMT, 1 (67 mm), LACM 20598.
Stn. 12491, 20 Nov. 1968, 29° N/118° W, 910 m, 10-ft IKMT, 2 (61-65 mm), LACM 30609.
Stn. 13385, 28 Oct. 1969, 28° N/118° W, 780 m, 10-ft IKMT, 1 (68 mm), LACM 30886.

Smithsonian Oceanographic Sorting Center, RV *Anton Bruun*, Cruise III and VI:
Label no. 7033, 18 Aug. 1963, 4° N/60° E, 2,120 m, 10-ft IKMT, 1 (34 mm), LACM 31302.
Label no. 7057, 23 Aug. 1963, 5° S/60° E, 2,030 m, 10-ft IKMT, 1 (26 mm), LACM 31303.
Label no. 7083, 6 Sept. 1963, 29° S/60° E, 1,150 m, 10-ft IKMT, 7 (44-55 mm), LACM 31320.
Label no. 7173, 23 May 1964, 8° N/65° E, 2,850 m, 10-ft IKMT, 1 (44 mm), LACM 31344.
Label no. 7177, 23 May 1964, 7° N/65° E, 940 m, 10-ft IKMT, 1 (36 mm), LACM 31345.
Label no. 7204, 27 May 1964, 2° N/65° E, 1,250 m, 10-ft IKMT, 1 (46 mm), LACM 31358.
Label no. 7217, 28 May 1964, 14° S/65° E, 2,250 m, 10-ft IKMT, 1 (53 mm), LACM 31361.
Label no. 7265, 4 June 1964, 12° S/64° E, 1,930 m, 10-ft IKMT, 1 (38 mm), LACM 31375.
Label no. 7273, 6 May 1964, 14° S/65° E, 880 m, 10-ft IKMT, 1 (47 mm), LACM 31376.
Label no. 7305, 24 June 1964, 24° S/65° E, 3,500 m, 10-ft IKMT, 1 (57 mm), LACM 31401.
Label no. 7312, 25 June 1964, 24° S/65° E, 1,100 m, 10-ft IKMT, 1 (56 mm), LACM 31404.

Office de la Recherche Scientifique et Technique Outre-Mer, Nouméa, New Caledonia:
RV *Caride*, Cruise I, stn. 36A, 23 Sept. 1968, 0°2′ N/137°51′ W, 950 m, 10-ft IKMT, 3 (51-60 mm), LACM 31439.
RV *Caride*, Cruise I, stn. 39A, 24 Sept. 1968, 0°14′ N/138°17′ W, 1,130 m, 10-ft IKMT, 1 (46 mm), LACM 31440.
RV *Caride*, Cruise I, stn. 69A, 29 Sept. 1968, 0°5′ N/144°41′ W, 580 m, 10-ft IKMT, 1 (32 mm), LACM 31446.
RV *Caride*, Cruise I, stn. 74A, 29 Sept. 1968, 0°/145°41′ W, 820 m, 10-ft IKMT, 1 (58 mm), LACM 31448.
RV *Caride*, Cruise I, stn. 77A, 30 Sept. 1968, 0°25′ N/146°17′ W, 1,110 m, 10-ft IKMT, 1 (48 mm), LACM 31450.
RV *Caride*, Cruise I, stn. 78A, 30 Sept. 1968, 0°2′ S/146°29′ W, 1,280 m, 10-ft IKMT, 1 (42 mm), LACM 31451.
RV *Caride*, Cruise III, stn. 17, 7 Feb. 1969, 11°17′ S/142°47′ W, 1,050 m, 10-ft IKMT, 1 (60 mm), LACM 31459.
RV *Caride*, Cruise III, stn. 18, 8 Feb. 1969, 11°7′ S/142°35′ W, 1,050 m, 10-ft IKMT, 1 (53 mm), LACM 31460.
RV *Caride*, Cruise III, stn. 60, 18 Feb. 1968, 0°12′ S/139°19′ W, 850 m, 10-ft IKMT, 1 (55 mm), LACM 31464.
RV *Caride*, Cruise III, stn. 64, 19 Feb. 1969, 0°/140°9′ W, 900 m, 10-ft IKMT, 1 (48 mm), LACM 31467.
RC *Caride*, Cruise III, stn. 68, 10 Feb. 1969, 0°/140°42′ W, 1,080 m, 10-ft IKMT, 1 (29 mm), LACM 31469.
RV *Caride*, Cruise III, stn. 122, 24 Feb. 1970, 0°3′N/147°2′ W, 1,100 m, 10-ft IKMT, 2 (45-51 mm), LACM 31478.
RV *Caride*, Cruise III, stn. 200, 2 March 1970, 0°1′ N/154°14′ W, 930 m, 10-ft IKMT, 1 (46 mm), LACM 31491.
RV *Caride*, Cruise III, stn. 204, 2 March 1970, 0°/154°25′ W, 1,160 m, 10-ft IKMT, 1 (34 mm), LACM 31492.
RV *Cyclone*, Cruise III, stn. 8, 4 May 1967, 2°13′ S/169°47′ E, 1,125 m, 10-ft IKMT, 1 (37 mm), LACM 31501.
RV *Cyclone*, Cruise III, stn. 17, 5 May 1967, 4°23′ S/169°52′ E, 1,090 m, 10-ft IKMT, 1 (51 mm), LACM 31505.
RV *Santo*, Cruise 68, stn. 6, 20 July 1968, 16°17′ S/166°40′ E, 1,395 m, 10-ft IKMT, 1 (52 mm), LACM 31528.

U.S. National Museum: Ocean Acre material:
Stn. 3-2N, 4 July 1967, 33° N/64°45′ W, 1,425 m, 10-ft IKMT, 1 (44 mm).
Stn. 3-11N, 5 July 1967, 33° N/64°40′ W, 1,920 m, 10-ft IKMT, 2 (53-58 mm).
Stn. 6-10B, 27 Apr. 1967, 31°59′ N/63°43′ W, 900 m, 10-ft IKMT, 1 (55 mm).
Stn. 6-24N, 30 Apr. 1967, 32°13′ N, 63°40′ W, 750 m, 10-ft IKMT, 1 (67 mm).
Stn. 7-13N, 8 Sept. 1967, 32°18′ N/63°30′ W, 1,500 m, 10-ft IKMT, 1 (36 mm).

Carlsberg Foundation, *Dana* collections:
Dana stn. 1156 VII, 25 Oct. 1921, 25° N/21° W, 2,000 m, S 150, 1 (37 mm).
Dana stn. 1159 II, 29 Oct. 1921, 18° N/24° W, 2,000 m, S 150, 1 (43 mm).
Dana stn. 1159 III, 29 Oct. 1921, 18° N/24° W, 1,500 m, S 150, 1 (35 mm).
Dana stn. 1181 III, 21 Nov. 1921, 13° N/57° W, 1,500 m, S 150, 1 (28 mm).
Dana stn. 1217 III, 29 Jan. 1922, 19° N/79° W, 1,500 m, S 150, 1 (45 mm).
Dana stn. 1342 I, 15 May 1922, 34° N/70° W, 2,250 m, E 300, 1 (43 mm).
Dana stn. 1365 IX, 8 June 1922, 32° N/42° W, 2,500 m, E 300, 1 (55 mm).

Zoological Institute, Academy of Sciences of the USSR, Leningrad:
RV *Lyra* stn. 50, 25 Mar. 1966, 3° N/120° W, 1,000 m, CN, 1 (43 mm).
RV *Lyra* stn. 3717, 9 Jan. 1957, 3° N/128° E, 1,250 m, CN, 1 (35 mm).
RV *Vitiaz* stn. 4183, 6 Dec. 1958, 40° N/127° W, 675 m, CN, 1 (65 mm).
RV *Vitiaz* stn. 4189, 7 Dec. 1958, 40° N/133° W, 1,000 m, CN, 1 (49 mm).
RV *Vitiaz* stn. 4939, 4 Feb. 1961, 9° N/87° E, 1,000 m, CN, 1 (39 mm).

National Institute of Oceanography, Surrey, England:
NIO stn. 4687, 30 Aug. 1961, 29°57′ N/32°3′ W, 800 m, IKMT, 1 (50 mm).
NIO stn. 4746, 30 Sept. 1961, 29°59′ N/22°56′ W, 1,100 m, IKMT, 2 (38-44 mm).
NIO stn. 5799, 19 Oct. 1965, 28°9′ N/14°9′ W, 675 m, IKMT, 1 (48 mm).
NIO stn. 5810, 7 Nov. 1965, 28°4′ N/13°51′ W, 800 m, IKMT, 1 (28 mm).
NIO stn. 5813, 10 Nov. 1965, 28°5′ N/14°11′ W, 950 m, IKMT, 1 (56 mm).
NIO stn. 6687, 7 Mar. 1968, 20°37′ N/22°56′ W, 1,000 m, RMT8, 1 (56 mm).
NIO stn. 7072, 30 Oct. 1969, 20°27′ N/25°32′ W, 1,000 m, RMT8, 2 (32-55 mm).
NIO stn. 7079, 3 Nov. 1969, 17°40′ N/27°6′ W, 1,000 m, RMT8, 1 (24 mm).
NIO stn. 7089 #54, 22 Nov. 1969, 17°47′ N/25°22′ W, 1,000 m, RMT8, 2 (54-77 mm).
NIO stn. 7089 #55, 22 Nov. 1969, 17°47′N/25°22′ W, 2,000 m, RMT8, 1 (46 mm).

British Museum of Natural History:
Rosaura collection, 26 June 1969, 17° N/86° W, 1,100 m, S 200, 1 (57 mm).
Rosaura collection, 26 June 1969, 11° N/76° W, 1,200 m, S 200, 1 (46 mm).

National Marine Fisheries Service, RV *Horizon*:
Cruise H6204 stn. 120-70, 23 Apr. 1962, 26° N/117° W, 1,676 m, 10-ft IKMT, 1 (65 mm).

Woods Hole Oceanographic Institution:
RHB stn. 977, 26 Feb. 1963, 1° S/27° W, 10-ft IKMT, 1,100 m, 1 (65 mm).
RHB stn. 979, 28 Feb. 1963, 3° S/29° W, 10-ft IKMT, 1,100 m, 1 (57 mm).
RHB stn. 1603, 6 Oct. 1967, 39°46′ N/70°30′ W, 10-ft IKMT, 1,000 m, 1 (65 mm).

Taaningichthys paurolychnus

University of Southern California, RV *Velero IV*:
Stn. 10675, 28 Aug. 1965, 29° N/118° W, 1,625 m, 10-ft IKMT, 1 (44 mm), LACM 9350.
Stn. 11187, 2 Aug. 1966, 29° N/118° W, 1,720 m, 10-ft IKMT, 1 (87 mm), LACM 9567.
Stn. 11257, 21 Oct. 1966, 29° N/118° W, 940 m, 10-ft IKMT, 1 (77 mm), LACM 9408.
Stn. 11628, 18 Aug. 1967, 32° N/119° W, 1,300 m, 10-ft IKMT, 1 (33 mm), LACM 9693.
Stn. 12331, 24 Aug. 1968, 29° N/118° W, 1,100 m, 10-ft IKMT, 1 (55 mm), LACM 30284.
Stn. 12340, 26 Aug. 1968, 32° N/118° W, 1,130 m, 10-ft IKMT, 1 (17 mm), LACM 30591.
Stn. 12475, 18 Nov. 1968, 28° N/119° W, 900 m, 10-ft IKMT, 1 (42 mm), LACM 30606.
Stn. 12483, 19 Nov. 1968, 28° N/119° W, 2,080 m, 10-ft IKMT, 3 (52-81 mm), LACM 30382.
Stn. 12592, 15 Jan. 1969, 32° N/120° W, 1,950 m, 10-ft IKMT, 3 (23-82 mm), LACM 30429.
Stn. 12593, 16 Jan. 1969, 32° N/120° W, 1,920 m, 10-ft IKMT, 1 (91 mm), LACM 30430.
Stn. 12594, 16 Jan. 1969, 32° N/120° W, 1,250 m, 10-ft IKMT, 1 (79 mm), LACM 30431.
Stn. 12786, 16 Mar. 1969, 32° N/118° W, 1,350 m, 10-ft IKMT, 1 (66 mm), LACM 30423.
Stn. 12791, 17 Mar. 1969, 32° N/118° W, 1,200 m, 10-ft IKMT, 1 (64 mm), LACM 30428.

Smithsonian Oceanographic Sorting Center, RV *Anton Bruun*, Cruise III and VI:
Label no. 7057, 23 Aug. 1963, 4° S/60° E, 2,030 m, 10-ft IKMT, 1 (51 mm), LACM 31303.

National Marine Fisheries Service, RV *Horizon*:
Cruise H6204 stn. 60.60, 26 Mar. 1962, 37° N/123° W, 1,863 m, IKMT, 1 (86 mm).
Cruise H6204 stn. 60.140, 29 Mar. 1962, 35° N/129° W, 1,863 m, IKMT, 1 (77 mm).
Cruise H6204 stn. 80.90, 18 Mar. 1962, 33° N/123° W, 2,234 m, IKMT, 1 (29 mm).
Cruise H6204 stn. 100.60, 13 Apr. 1962, 31° N/119° W, 1,676 m, IKMT, 1 (68 mm).
Cruise H6204 stn. 100.80, 13 Apr. 1962, 30° N/120° W, 1,676 m, IKMT, 1 (82 mm).

Scripps Institution of Oceanography:
SIO 54-95, 23 June 1954, 23° N/119° W, 2,500 m, 10-ft IKMT, 1 (49 mm).
SIO 60-283, 12 Aug. 1960, 28° N/135° W, 3,000 m, 10-ft IKMT, 1 (44 mm).
SIO 60-284, 13 Aug. 1960, 29° N/132° W, 3,000 m, 10-ft IKMT, 1 (71 mm).
SIO 64-11, 30 Jan. 1964, 24° N/113° W, 5,300 m, 10-ft IKMT, 1 (78 mm).
SIO 66-31, 5 Apr. 1966, 29° N/117° W, 4,000 m, 10-ft IKMT, 1 (84 mm).
SIO 67-52, 22 Apr. 1967, 30° N/117° W, 4,000 m, 10-ft IKMT, 1 (80 mm).

SIO 67-102, 10 June 1967, 35° N/123° W, 2,200 m, 10-ft IKMT, 2 (65-71 mm).
SIO 70-19, 17 Dec. 1969, 31° N/119° W, 4,000 m, 10-ft IKMT, 1 (67 mm).
SIO 70-20, 17 Dec. 1969, 31° N/119° W, 4,000 m, 10-ft IKMT, 2 (79-95 mm).

National Institute of Oceanography, Surrey, England:
NIO sta. 7089 #55, 22 Nov. 1969, 17°47′ N/25°22′ W, RMT8, 3 (45-73).

Zoological Institute, Academy of Sciences of the USSR, Leningrad:
RV *Akademik Kurchatov* stn. 233, 13 Sept. 1968, 17° S/86° W, 2,000 m, CN, 1 (87 mm), 39908.

Zoological Museum, University of Copenhagen:
Dana stn. 1217 I, 29 Jan. 1922, 19° N/79° W, 2,000 m, E 300, 1 (57 mm), P2330669.

Museu Municipal do Funchal, Madeira:
RV *Discovery* 4742, 20 Sept. 1961, 32°42′ N/16°32′ W, 1,700 m, IKMT, 1 (49 mm), MMF 22115.

SOME LIFE HISTORY CHARACTERISTICS OF COHO SALMON OF THE KARLUK RIVER SYSTEM, KODIAK ISLAND, ALASKA

BENSON DRUCKER[1]

ABSTRACT

This paper contains data on some life history characteristics of the coho salmon of the Karluk River system, Kodiak Island, Alaska: age, fecundity, length, and egg size of adults; and migration characteristics, age, and size of smolts. The greater age at maturity of Karluk coho salmon (4 and 5 years) because of the longer freshwater residence of the juveniles is unique among reported North American stocks and may result in greater freshwater mortality but less marine mortality because the smolts are larger when they enter the ocean. Fecundity of Karluk coho salmon also differs from that reported for other North American stocks in that they are extremely fecund—more similar to Asiatic stocks of the Kamchatka Peninsula.

Coho salmon, *Oncorhynchus kisutch*, are widely distributed along the Pacific coast of North America and occur in commercially harvestable quantities from northern California to northwestern Alaska. About one-third of the total North American commercial catch comes from Alaska waters, where from 1960 to 1968 the average annual catch of 16 million pounds was valued at almost $3.5 million to the fishermen.[2] The amount of biological research on coho salmon in Alaska is small, and published scientific reports on Alaska coho salmon stocks are very few.

In this paper I present data on some life history characteristics of the coho salmon of the Karluk River system. This system is located on the southwest side of Kodiak Island, Alaska, at approximately lat 57° N and long 154° W and includes Karluk Lake, tributaries to the lake, Thumb and O'Malley Lakes, and Karluk River (Figure 1). Information is presented on age, fecundity, length, and egg size of coho salmon adults; and migration characteristics, age, and

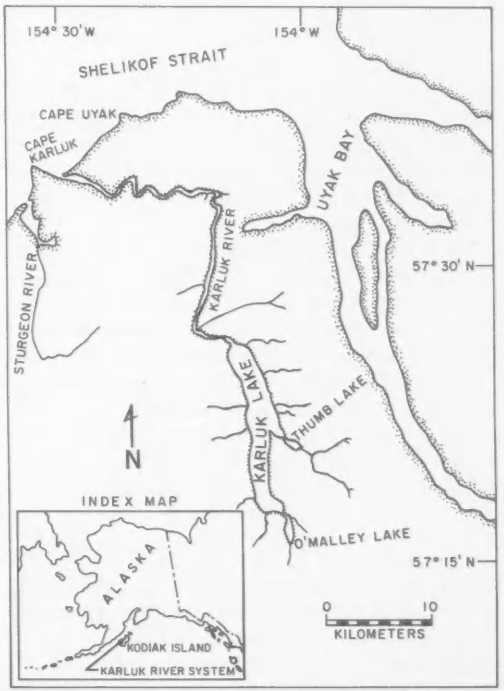

FIGURE 1.—The Karluk River system, Kodiak Island, Alaska.

[1] National Marine Fisheries Service, Auke Bay Fisheries Laboratory, Auke Bay, Alaska 99821; present address: National Marine Fisheries Service, Technical Advisory Division, Interior Building, Washington, D.C. 20235.

[2] Nelson, Richard C. 1968. Alaska catch and production, commercial fisheries statistics. Alaska Dep. Fish Game, Stat. Leafl. 17, 29 p. (Unpublished.)

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FISHERY BULLETIN: VOL. 70, NO. 1, 1972.

size of coho salmon smolts. These life history features of Karluk coho salmon are compared with those reported for various coho salmon stocks from other areas on both the Asiatic and North American sides of the Pacific Ocean. In addition, the effect of a prolonged juvenile freshwater residence, a feature unique to the Karluk system, on freshwater and marine survival is discussed. All of the data on Karluk coho salmon were collected incidentally during studies of sockeye salmon, *O. nerka*, the dominant salmon species in the Karluk system; much of the information on other Alaska stocks is from unpublished administrative and progress reports.

Because I intend to discuss differences between coho salmon in the Karluk system and those in other areas, a description of general features of the life cycle of coho salmon stocks is appropriate. Typically, the adults enter streams and rivers from late summer to November and spawn in late fall and early winter. Some Asiatic stocks, however, spawn as late as mid-March (Smirnov, 1960). The progeny emerge as fry in the spring following spawning and reside in rivers or lakes for 1 or 2 years before going to sea as smolts. In some areas the seaward smolt migration begins in late winter (Chapman, 1961; Smoker, 1953), but in most areas it takes place from April to August (Godfrey, 1965). The salmon grow rapidly in the ocean, and the adults return to the streams and rivers to spawn 12 to 18 months later. However, a significant percentage of male coho salmon, particularly in their southern range of distribution in North America (California), mature precociously (6 to 9 months after they enter salt water) and return to spawn the same year that they migrated to sea (Shapovalov and Taft, 1954). These fish are known as jack salmon.

METHODS

The data for adult coho salmon of the Karluk system were obtained from fish from the 1966 escapement that were captured at the adult counting weir or caught by sport fishermen at the outlet of Karluk Lake about 300 yards upstream from the weir site. All fish were measured for length (mideye to fork of tail) with a caliper to the nearest millimeter. Mideye-fork length was used because of morphological changes that occur as the fish matures, particularly the elongation of the snout. Ovaries for fecundity samples were removed from all females and were preserved in 10% Formalin solution for at least 48 hr. The eggs were then hand-counted to get total egg counts. The diameters of some eggs from the fecundity samples were measured. These eggs were removed directly from the ovary, water hardened, and placed in Stockard's solution. The diameters were then measured with a vernier measuring microscope calibrated to 0.01 mm. The ages of adult fish were determined by reading scales that had been taken halfway between the lateral line and the posterior insertion of the dorsal fin.

The data for smolts were obtained from fish captured in 1956, 1965, and 1968 in fyke nets fished on the downstream side of the adult counting weir. Fork lengths were taken to the nearest millimeter with a steel millimeter ruler, and weights were taken to the nearest tenth of a gram on a triple-beam balance. As with the adults, the ages of smolts were determined from scales taken halfway between the lateral line and the posterior insertion of the dorsal fin.

AGE OF COHO SALMON

The average age composition of coho salmon for several systems in northern and southern latitudes of North America and Asia is shown in Table 1. The differences from the northern to southern latitudes in age composition is similar to that noted by Marr (1943) and possibly represent a geographic cline.

The Karluk system had three freshwater age classes,[3] two of which were decidedly predominant (Table 1). The three age classes, 4_3, 5_4, and 6_5, designate fish that went to sea in their third, fourth, and fifth years of life and returned to spawn after being at sea for about 1 year.

[3] Age classes are designated according to the system developed by Gilbert and Rich (1927). A 4_3 coho salmon is in its fourth year of life. It went to sea as a smolt at the beginning of its third year, having spent two growing seasons in fresh water.

TABLE 1.—Age class composition of stocks of coho salmon from North America and Asia, arranged geographically from north to south.

Area	Percent coho salmon in age class—										Reference
	2_1	2_3	3_1	3_2	3_3	4_1	4_2	4_3	5_3	5_4	6_3	
North America												
Nome River, Alaska	--	--	--	29.4	--	--	--	70.6	--	--	--	Godfrey (1965)
Unalakleet River, Alaska	--	--	--	37.9	--	--	--	62.1	--	--	--	Godfrey (1965)
Yukon River, Alaska	--	--	--	55.6	--	--	--	44.4	--	--	--	Godfrey (1965)
Yukon River, Alaska	--	--	--	38.7	--	--	--	58.1	--	3.2	--	Gilbert (1922)
Cook Inlet River, Alaska	--	--	--	40.0	--	--	--	60.0	--	--	--	Godfrey (1965)
Resurrection Bay, Alaska	--	--	--	30.3	--	--	--	68.8	--	0.9	--	Logan (1963,[1] 1964[2])
Bear Creek, Alaska	--	--	--	27.1	--	--	--	71.1	--	1.8	--	Logan (1964)[2]
Dairy Creek, Alaska	--	--	--	[3]83.3	--	--	--	16.7	--	--	--	Logan (1964)[2]
Mendenhall River, Alaska	--	--	--	12.0	8.0	--	--	80.0	--	--	--	([4])
Hood Bay Creek, Alaska	--	--	--	46.5	--	--	--	47.5	--	6.0	--	Armstrong (1970)
Karluk River, Alaska	--	--	--	--	--	--	--	56.9	--	41.7	1.4	Present study
Sashin Creek, Alaska	--	--	--	18.0	--	--	--	77.0	--	5.0	--	Crone (1968)
Port Herbert, Alaska	--	--	--	20.0	--	--	--	76.0	--	4.0	--	Crone (1968)
Stikine River, Alaska	--	--	--	45.2	--	--	1.0	51.9	1.9	--	--	Godfrey (1965)
Chignik River, Alaska	--	--	--	23.2	--	--	--	72.4	--	4.4	--	Israel (1933)
Ketchikan River, Alaska	--	--	--	70.8	--	--	--	29.2	--	--	--	Godfrey (1965)
Quatsino Bay, British Columbia	--	2.0	--	95.0	--	--	3.0	--	--	--	--	Godfrey (1965)
Fraser River, British Columbia	2.6	--	0.7	96.5	--	--	0.2	--	--	--	--	Godfrey (1965)
Georgia Strait, British Columbia	1.5	0.6	0.4	97.1	--	--	0.4	--	--	--	--	Godfrey (1965)
West coast, Vancouver Island, British Columbia	1.3	--	0.6	97.5	--	--	0.4	0.2	--	--	--	Godfrey (1965)
Langara Island, Georgia Strait, British Columbia	0.1	0.1	0.2	97.9	Tr.	0.1	0.7	0.9	--	--	--	Pritchard (1940)
Columbia River, Wash.	--	6.1	--	83.9	0.3	--	--	9.7	--	--	--	Marr (1943)
Waddell Creek, Calif.	--	18.4	--	81.6	--	--	--	--	--	--	--	Shapovalov and Taft (1954)
Asia												
East coast of Kamchatka, USSR:												
Kamchatka River	--	1.2	--	55.7	--	--	--	43.1	--	--	--	Godfrey (1965); Gribanov (1948)
Lake Ushki	--	Tr.	--	4.3	Tr.	--	--	92.9	--	2.8	--	Gribanov (1948)
Kyrganik River	--	Tr.	--	93.6	Tr.	--	--	6.4	--	--	--	Gribanov (1948)
Paratunka River	--	Tr.	--	57.4	Tr.	--	--	42.6	--	--	--	Gribanov (1948)
Avachin Gulf, Solevarka Bay	--	Tr.	--	80.2	Tr.	--	--	19.8	--	--	--	Gribanov (1948)
Kalyger River	--	Tr.	--	27.5	Tr.	--	--	72.5	--	--	--	Gribanov (1948)
West coast of Kamchatka, USSR:												
Kikhchik River	--	Tr.	--	100.0	Tr.	--	--	--	--	--	--	Gribanov (1948)
Bolshaya River	--	--	Tr.	69.3	Tr.	--	--	30.1	--	--	--	Godfrey (1965); Gribanov (1948); Semko (1954)
Ozernaia River	--	--	Tr.	100.0	Tr.	--	--	--	--	--	--	Gribanov (1948)
Kukhtui River (Okhotsk)	--	--	--	32.8	--	--	--	67.2	--	--	--	Godfrey (1965)

[1] Logan, Sidney M. 1963. Silver salmon studies in the Resurrection Bay area. *In* Dingell-Johnson project report, 1962-63, Vol. 4: 175-194, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)
[2] Logan, Sidney M. 1964. Silver salmon studies in the Resurrection Bay area. *In* Dingell-Johnson project report, 1963-64, Vol. 5: 133-151, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)
[3] The high percentage of age 3_2 fish is atypical and not representative of Resurrection Bay streams. Dairy Creek juveniles are reared in a brackish water lagoon rather than in the stream itself, resulting in 1-year smolts. (Personal communication, Sidney Logan, Area Management Biologist, Alaska Department of Fish and Game, Soldotna, Alaska, March 15, 1971.)
[4] Collected by author in 1966.

Fifty-seven percent of the Karluk fish had migrated in their third year and 42% in their fourth year; only 1% had migrated in their fifth year (Table 1). Although the freshwater residence of fish in the Karluk escapement varied from 2 to 4 years, Karluk coho salmon, like those in all other systems, returned to spawn after being at sea for 12 to 18 months.

The presence of large numbers of fish (42%) that had spent 3 years in freshwater residence (age class 5_4) is unique to the Karluk system. Fish of age class 5_4 have been found in other Alaska river systems, i.e., the Yukon River (Gilbert, 1922), Resurrection Bay and Bear Creek (see footnotes 1 and 2, Table 1), Hood Bay Creek (Armstrong, 1970), Sashin Creek and Port Herbert (Crone, 1968), and Chignik River (Israel, 1933); but the proportion of 5_4 fish in the total runs to these systems is small—usually less than 5% (Table 1).

The age composition of stocks of coho salmon from systems on the Kamchatka Peninsula,

USSR, is similar to that of coho salmon in the northern areas of the west coast of North America. The main age classes are 3_2 and 4_3 (Table 1). The ratio of one age class to the other varies, however, from year to year and from area to area (Gribanov, 1948; Semko, 1954).

An additional comparison of the age composition of coho salmon from northern to southern latitudes is shown in Figure 2, which gives the percent age composition of the major age classes from five geographical areas along the west coast of North America. In California, the southern limit of the range of coho salmon, the major age class is 3_2, but jack salmon (age 2_2) contribute significantly to the runs. The 3_2 age class is still dominant in Washington, but the number of jack salmon is less and 4_3 fish are starting to appear. North of Washington to central British Columbia, more than 95% of the fish are age 3_2, and there are only traces of other age classes, mainly the 4_3 class. From central British Columbia and northward through Alaska, the primary age class is 4_3; 3_2 fish are the secondary class and 5_4 fish are found in small numbers. In Alaska, the increase in total age is the result of juvenile coho salmon residing an additional year in fresh water before migrating to sea. Possible exceptions to the dominance of the 4_3 age class in Alaska are the Ketchikan River, Dairy Creek, Yukon River, and Karluk River systems (Table 1). In the first three river systems, 3_2 fish are the dominant age class and 4_3 fish the secondary class. The sizes of the samples from these systems were small, however (less than 25 fish). In the Karluk system, although 4_3 fish were dominant, 5_4 fish rather than 3_2 fish were the secondary age class (Figure 2).

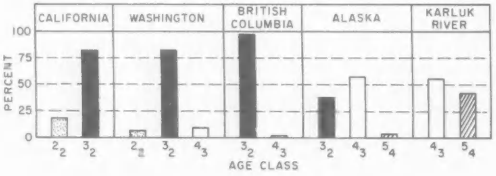

FIGURE 2.—Average age composition of coho salmon runs along the west coast of North America by geographical area (minor age classes omitted).

The presence of older fish (5_4) in northern latitudes may be a result of the juveniles being reared in lakes rather than rivers. Typically, coho salmon spawn in rivers or tributaries to rivers and the emerging fry reside in these areas until they migrate to sea. In contrast, in some Alaska river systems where 5_4 fish are part of the run (Table 1 and Figure 2), the juveniles migrate from spawning grounds to lakes before migrating to sea. It appears that some of the juveniles that reside in lakes (lake type) go to sea at an older age than those that reside in rivers (river type).[4]

NUMBER AND SIZE OF EGGS

In this section, information is presented on fecundity (number of eggs contained in a female) as a function of latitude and length, the relative numbers of eggs in right and left ovaries, and egg size in relation to length and fecundity. Fecundity and factors related to it form the basis for determining the reproductive potential of a spawning stock and subsequent survival from egg to young. Knowledge of variations in fecundity and egg size is of increasing importance in fish stocking and fish rehabilitation programs. Size of egg may be useful in predicting the condition, or hardiness, of developing fry. Because the fecundity of fish differs among geographic areas, the reproductive potential must be determined for each stock.

FECUNDITY AS A FUNCTION OF LATITUDE

The average fecundity for both North American and Asiatic stocks of coho salmon is considerably higher in fish from northern latitudes than in those from southern latitudes (Table 2 and Figure 3). Coho salmon from Alaska river systems (with the exception of the two small samples from Port Herbert and Sashin Creek)

[4] Personal communication, 1969, Charles J. DiCostanzo, Chief, Salmon Investigations, National Marine Fisheries Service, Auke Bay Fisheries Laboratory, Auke Bay, Alaska 99821.

TABLE 2.—Average fecundity of coho salmon stocks from North American and Asiatic river systems, arranged geographically from north to south.

Area	Latitude	Average number of eggs	Reference
North America			
Swanson River, Alaska	61° N	3,378	Engel (1966)[1]
Bear Creek, Alaska	60° N	4,115	Lawler (1963,[2] 1964[3])
Dairy Creek, Alaska	60° N	4,177	Engel (1965),[4]; Lawler (1963)[2]
Karluk River, Alaska	57° N	4,706	Present study
Pasagshak River, Alaska	57° N	4,510	Marriott (1968)[5]
Sashin Creek, Alaska	56° N	2,868	Crone (1968)
Port Herbert, Alaska	56° N	2,565	Crone (1968)
Namu River, British Columbia	54° N	3,002	Foerster and Pritchard (1936)
Fraser River, British Columbia	53° N	3,152	Foerster and Pritchard (1936)
Nile Creek, British Columbia	49° N	2,310	Wickett (1951)
Cultus Lake Hatchery, British Columbia	49° N	2,300	Foerster and Ricker (1953)
Port John, British Columbia	49° N	2,313	Hunter (1948)
Cowichan River, British Columbia	48° N	2,329	Neave (1948)
Oliver Creek, British Columbia	48° N	2,267	Foerster (1944)
Beadnell Creek, British Columbia	48° N	2,789	Foerster (1944)
Seattle, Wash.	47° N	3,141	Allen (1958)
Minter Creek, Wash.	47° N	2,447	Salo and Bayliff (1958)
Fall Creek, Alsea River, Ore.	44° N	1,983	Koski (1966)
Scott Creek, Calif.	37° N	2,336	Shapovalov and Taft (1954)
Asia			
East coast of Kamchatka, USSR:			
Ushki Hatchery	56° N	5,282	Gribanov (1948)
Kamchatka River	56° N	4,883	Gribanov (1948)
Paratunka River	53° N	4,350	Gribanov (1948)
West coast of Kamchatka, USSR:			
Bolshaya River	53° N	4,638	Semko (1954)
Sakhalin Island, USSR:			
Tymi River	52° N	4,570	Smirnov (1960)

[1] Engel, Larry J. 1966. Egg-take investigations in Cook Inlet drainage and Prince William Sound. *In* Federal aid in fish restoration, 1965-66 progress report, Vol. 7: 109-116, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)

[2] Lawler, Robert E. 1963. Silver salmon egg taking investigations in Cook Inlet drainage. *In* Dingell-Johnson project report, 1962-63, Vol. 4: 161-173, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)

[3] Lawler, Robert E. 1964. Egg take investigations in Cook Inlet and Prince William Sound. *In* Dingell-Johnson project report, 1963-64, Vol. 5: 123-132, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)

[4] Engel, Larry J. 1965. Egg take investigations in Cook Inlet drainage and Prince William Sound. *In* Dingell-Johnson project report, 1964-65, Vol. 6: 155-163, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)

[5] Marriott, Richard A. 1968. Inventory and cataloging of the sport fish waters in southwest Alaska. *In* Federal aid in fish restoration, 1967-68 progress report, Vol. 9: 81-93. Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)

are more fecund than coho salmon from more southerly areas in North America (Figure 3). Stocks of coho salmon from Asiatic river systems are extremely fecund, even more so than North American stocks in more northerly latitudes. The high fecundity of Karluk River coho salmon more closely resembles the fecundity of Asiatic stocks than North American ones.

Contrary to these findings for coho salmon, Rounsefell (1957) suggests that for the genus *Oncorhynchus*, salmon in southern latitudes may be more fecund than those in northern latitudes because of ". . . the higher age at maturity, and therefore slower growth rates, from south to north." Rounsefell found that the amount of time juvenile sockeye salmon spent in fresh water had no effect on fecundity, but the amount of time the adults spent at sea did have an effect: adult sockeye salmon that spent 2 years at sea had higher fecundity counts than fish of the same size that spent 3 years at sea. With coho salmon, however, the greater age at maturity is not due to increased time in the ocean but to increased time in fresh water.

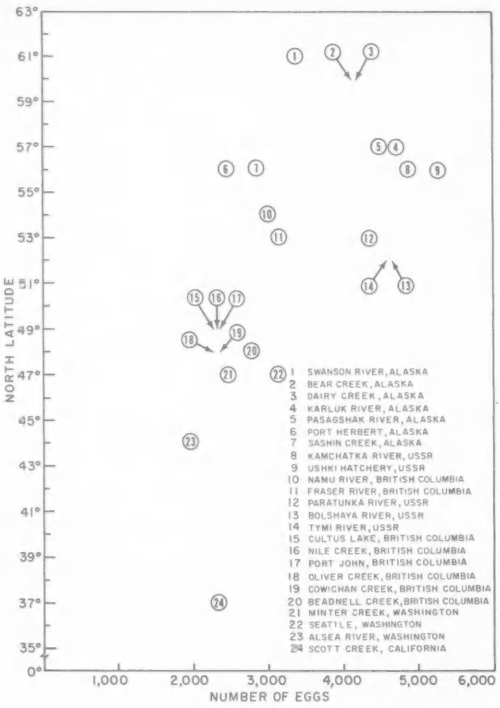
NORTH LATITUDE
NUMBER OF EGGS
1 SWANSON RIVER, ALASKA
2 BEAR CREEK, ALASKA
3 DAIRY CREEK, ALASKA
4 KARLUK RIVER, ALASKA
5 PASAGSHAK RIVER, ALASKA
6 PORT HERBERT, ALASKA
7 SASHIN CREEK, ALASKA
8 KAMCHATKA RIVER, USSR
9 USHKI HATCHERY, USSR
10 NAMU RIVER, BRITISH COLUMBIA
11 FRASER RIVER, BRITISH COLUMBIA
12 PARATUNKA RIVER, USSR
13 BOLSHAYA RIVER, USSR
14 TYMI RIVER, USSR
15 CULTUS LAKE, BRITISH COLUMBIA
16 NILE CREEK, BRITISH COLUMBIA
17 PORT JOHN, BRITISH COLUMBIA
18 OLIVER CREEK, BRITISH COLUMBIA
19 COWICHAN CREEK, BRITISH COLUMBIA
20 BEADNELL CREEK, BRITISH COLUMBIA
21 MINTER CREEK, WASHINGTON
22 SEATTLE, WASHINGTON
23 ALSEA RIVER, WASHINGTON
24 SCOTT CREEK, CALIFORNIA

FIGURE 3.—Average fecundity of various stocks of coho salmon from North America and Asia.

FECUNDITY AS A FUNCTION OF LENGTH

The presence of a positive relation between fecundity and length in the genus *Oncorhynchus* is well known (Gilbert and Rich, 1927; Foerster and Pritchard, 1941; Allen, 1958; Hartman and Conkle, 1960). For fish in general, the relation of fecundity to length is logarithmic ($\hat{Y} = aX^b$) over a wide range of lengths. For salmon, however, the narrow range in length at maturity permits this relation to be described adequately by a straight line of the form $\hat{Y} = a + bX$ (Foerster and Pritchard, 1941; Rounsefell, 1957).

I counted the total number of eggs in 49 coho salmon from the Karluk River and calculated the relation between number of eggs and mideye-fork length by the method of least squares. The result may be expressed by the equation $\hat{Y} = -7{,}503.55 + 195.51X$, where $\hat{Y}$ is the estimate of number of eggs and X is the mideye-fork length of female salmon (Figure 4). The mean number of eggs for the sample was 4,706 (range 1,724 to 6,906); the mean length was 62.1 cm (range 46.6 to 69.8 cm).

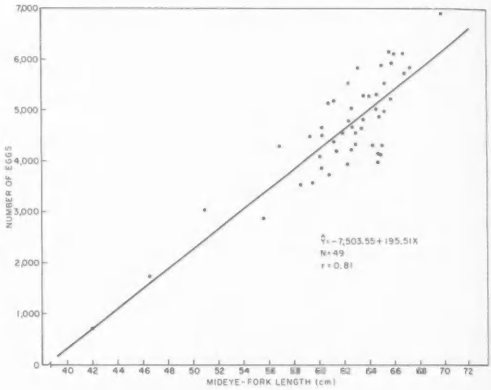

FIGURE 4.—Relation of fecundity to length of coho salmon sampled at Karluk weir, 1966.

It is difficult to determine if the high fecundity of coho salmon of the Karluk system (Figure 3) is due to greater fecundity per unit length or simply to the fact that coho salmon from Karluk are very large. The average lengths of female coho salmon from various spawning streams along the Pacific coast of North America are quite variable and do not seem to follow any set geographic pattern (Table 3). Moreover, Karluk fish were measured from mideye to fork of tail, and direct comparisons of lengths with coho salmon from other areas are difficult to make because of variability in the types of measurements used. For instance lengths reported from areas other than Karluk include tip of snout to fork of tail (fork length), tip of snout to tip of tail (total length), and tip of snout to base of tail (standard length).

TABLE 3.—Average lengths of female coho salmon from river systems along the Pacific coast of North America and Asia, arranged geographically from north to south.

Area	Average length				Reference
	Fork	Total	Standard	Mideye-fork	
	cm	*cm*	*cm*	*cm*	
North America					
Yukon River, Alaska	63.4	--	--	--	Gilbert (1922)
Swanson River, Alaska	62.0	--	--	--	Engel (1966)[1]
Resurrection Bay, Alaska	67.2	--	--	--	Logan (1965)[2]
Dairy Creek, Alaska	72.8	--	--	--	Engel (1965)[3]
Brooks River, Alaska	--	58.8	--	--	(4)
Karluk River, Alaska	--	--	--	62.1	Present study
Sashin Creek, Alaska	70.5	--	--	--	Crone (1968)
Port Herbert, Alaska	67.8	--	--	--	Crone (1968)
Namu River, British Columbia	--	69.0	--	--	Foerster and Pritchard (1936)
Fraser River, British Columbia	--	64.0	--	--	Foerster and Pritchard (1936)
Seattle, Wash.	63.4	--	--	--	Allen (1958)
Minter Creek, Wash.	--	--	62.1	--	Salo (1955)
Columbia River, Wash.	74.6	--	--	--	Marr (1943)
Deer Creek, Oreg.	70.7	--	--	--	Koski (1966)
Flynn Creek, Oreg.	69.4	--	--	--	Koski (1966)
Needle Branch, Oreg.	67.6	--	--	--	Koski (1966)
Scott Creek, Calif.	66.3	--	--	--	Shapovalov and Taft (1954)
Waddell Creek, Calif.	63.9	--	--	--	Shapovalov and Taft (1954)
Asia					
East coast of Kamchatka, USSR:					
Kamchatka River	60.9	--	--	--	Gribanov (1948)
Kyrganik River	68.1	--	--	--	Gribanov (1948)
Kalyger River	61.0	--	--	--	Gribanov (1948)
Avachin Gulf	55.4	--	--	--	Gribanov (1948)
Paratunka River	59.4	--	--	--	Gribanov (1948)
West coast of Kamchatka, USSR:					
Kikhchik River	58.6	--	--	--	Gribanov (1948)
Bolshaya River	57.4	--	--	--	Gribanov (1948)
Ozernaia River	62.6	--	--	--	Gribanov (1948)

[1] See footnote 1, Table 2.
[2] Logan, Sidney M. 1965. Silver salmon studies in the Resurrection Bay area. *In* Dingell-Johnson project report, 1964-65, Vol. 6: 129-145, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)
[3] Lawler, Robert E. 1964. Egg take investigations in Cook Inlet and Prince William Sound. *In* Dingell-Johnson project report, 1963-64, Vol. 5: 123-132, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)
[4] Eicher, George J., Jr. The effects of laddering a falls in a salmon stream. National Marine Fisheries Service, Auke Bay Fisheries Laboratory, Auke Bay, Alaska, 5 p. (Unpublished.)

NUMBER OF EGGS IN RIGHT AND LEFT OVARIES

The numbers of eggs in the right and left ovaries of the genus *Oncorhynchus* are usually quite variable. Rounsefell (1957) noted that although the rate of maturation of eggs from Karluk Lake sockeye salmon was the same in both ovaries of the same fish, the number of eggs in each ovary varied. Eguchi and his co-workers (Rounsefell, 1957) found no significant differences in the numbers of eggs in the two ovaries in chum salmon, *O. keta*, in Japanese waters. Helle (1970) found the same lack of a significant difference in a sample of pink salmon, *O. gorbuscha*, from Olsen Bay, Alaska, in 1963. Sockeye salmon from Brooks Lake, Alaska, in 1957 and 1958 and from Karluk Lake in 1958 had more eggs in the left ovary than in the right (Hartman and Conkle, 1960). At Bare Lake, Alaska, sockeye salmon had more eggs in the right ovary than in the left (Nelson, 1959).

I compared the numbers of eggs from the right and left ovaries of Karluk River coho salmon (Table 4) by means of a t test for paired observations. The differences between the numbers of eggs in the right and left ovaries were significant ($t = 2.60$; df $= 31$; $P = 0.05$). In 31 fecundity samples, 71% had more eggs in the right ovary than the left. I could not find comparable information on comparisons between the numbers of eggs in the ovaries of coho salmon from other areas.

TABLE 4.—Numbers of eggs in right and left ovaries from coho salmon collected at the outlet to Karluk Lake, 1966.

Sample number	Mideye-fork length (cm)	Number of eggs		
		Right ovary	Left ovary	Total
1	50.9	1,640	1,403	3,043
2	61.4	2,265	1,918	4,183
3	65.0	3,005	2,876	5,881
4	56.9	2,213	2,083	4,296
5	62.7	2,322	2,337	4,659
6	65.6	3,001	3,147	6,148
7	69.8	3,559	3,347	6,906
8	64.7	2,258	1,884	4,142
9	62.6	2,546	2,501	5,047
10	60.2	2,433	2,220	4,653
11	59.3	2,243	2,225	4,468
12	60.2	2,331	2,161	4,492
13	62.3	2,481	2,283	4,764
14	61.2	2,620	2,539	5,159
15	60.1	2,067	2,000	4,067
16	63.5	2,581	2,221	4,802
17	64.5	2,473	2,546	5,019
18	67.2	2,604	3,233	5,837
19	60.2	2,044	1,813	3,857
20	65.2	2,824	2,697	5,521
21	64.0	2,608	2,659	5,267
22	65.1	2,491	2,501	4,992
23	66.0	2,926	3,174	6,100
24	62.9	2,266	2,280	4,546
25	65.8	3,047	2,878	5,925
26	64.6	2,726	2,579	5,305
27	63.6	2,721	2,563	5,284
28	66.7	3,104	2,997	6,101
29	63.1	2,981	2,843	5,824
30	61.9	2,176	2,125	4,301
31	64.8	2,340	2,521	4,861
Average	63.0	2,545	2,469	5,015

RELATION OF EGG SIZE TO LENGTH AND TO FECUNDITY

The average diameter of eggs obtained from the fecundity samples from Karluk River was plotted against the length of the female coho salmon from which the samples were taken (Figure 5) to determine if there was a relation between the size of a female and the size of her eggs. The size of eggs increases as they mature, and so the eggs used had to be in the same stage of maturation. I therefore selected only females beginning to show secondary sexual characteristics and containing eggs that could not be readily expressed from the body cavity. For 25 females the eggs varied in size from 4.92 to 6.88 mm (mean 6.11 mm); lengths varied from 50.4 to 69.8 cm (mean 62.0 cm). No relation was found between the size of the egg and the length of the fish. Allen (1958) in his studies of coho salmon in Green River, Wash., also found no relation.

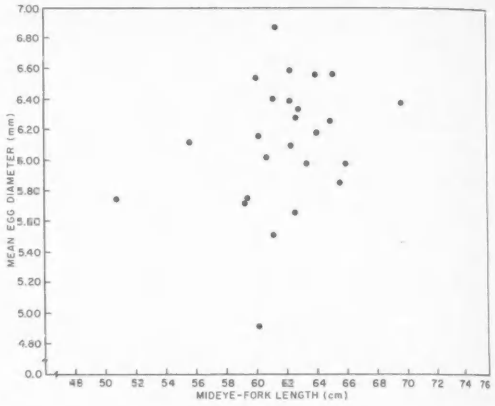

FIGURE 5.—Relation of mean egg diameter to mideye-fork length of female coho salmon, Karluk River, 1966.

The average diameters of eggs were plotted against number of eggs in individual fish to determine if a relation existed between the fecundity of a female and the size of her eggs (Figure 6). For 24 females, the egg diameter ranged

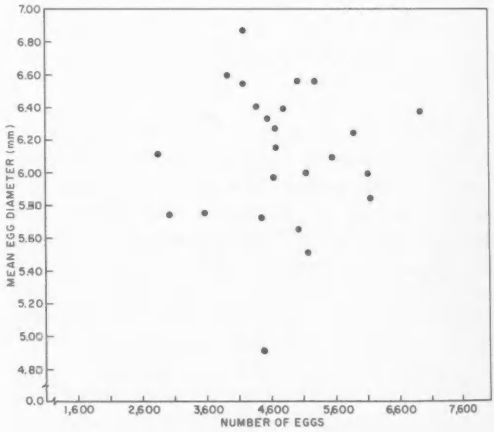

FIGURE 6.—Relation of mean egg diameter to number of eggs in female coho salmon, Karluk River, 1966.

from 4.91 to 6.87 mm (mean 6.11 mm); fecundity ranged from 2,855 to 6,906 (mean 4,766). No relation was found: eggs from a female with low fecundity were not necessarily large, nor were those from a female with high fecundity necessarily small. Allen (1958) reported similar findings.

Unlike the general relation that exists between fecundity and length (i.e., larger fish are more fecund), the size or fecundity of the females I sampled apparently had no relation to the size of the eggs. Large, fecund females had a wide range of egg sizes (Figure 5). Thus, the larger number of eggs in large females may be due to a larger body cavity that allows more eggs to develop rather than to the fish having smaller eggs.

COHO SALMON SMOLTS

Smolts of coho salmon, like those of other salmon that live for a while in fresh water before migrating to sea, migrate seaward at a particular season and under particular light intensities. This migration and the associated environmental factors and information on age and size of migrating smolts are discussed in this section.

SEASONAL MIGRATION

Coho salmon juveniles reside in Karluk Lake for 1 to 4 years before they migrate to sea as smolts. From 1961 to 1967 the migration began in mid-May and was usually over by early July (Figure 7).

Although most coho salmon migrate in the spring (Hamilton and Andrew, 1954; Taft, 1934; Gharrett and Hodges, 1950; Semko, 1954), several exceptions do exist. In the Paratunka River, Kamchatka Peninsula, the migration extends from the end of May to the end of August (Gribanov, 1948); in several streams in Oregon it extends from late winter to May (Chapman, 1961); in some streams in western Washington it runs from early winter to late spring (Smoker, 1953); and at Waddell Creek, Calif., small numbers of atypical migrants migrate in the fall and early winter (Shapovalov and Taft, 1954). The

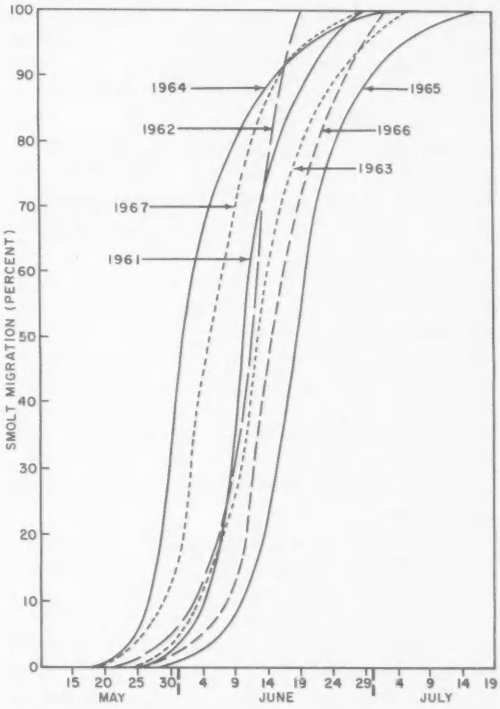

FIGURE 7.—Cumulative seasonal migration of coho salmon smolts from Karluk Lake, 1961-67.

number of coho salmon smolts involved in the early or late parts of these migrations, however, represents only a small percentage of the total number of smolts in each migration.

The warming of the water after the ice breaks up is of major importance in initiating the seaward migration of smolts. Hartman, Heard, and Drucker (1967) found this to be a major factor in the migration of sockeye salmon in lakes of southwestern Alaska; and Logan (see footnote 2, Table 1) found that the coho salmon smolt migration in Bear Lake, Alaska, did not start until the ice cover on the lake was gone and the water temperature had risen to 4.2° C. Ninety percent of the Bear Lake coho salmon smolts had migrated to sea when water temperatures ranged between 5° and 13.3° C. Coho salmon smolts apparently migrate over a greater

temperature range than sockeye salmon, whose migration generally ends when water temperatures reach about 10° C (see footnote 2, Table 1).

At Karluk Lake, for each year from 1961 to 1968 (excluding 1964) the date by which 50% of the coho salmon smolts had migrated was later than the comparable date for sockeye salmon smolts (Table 5). The difference in time of the two migrations ran from 6 to 19 days (average 11 days). Not only did more of the coho salmon smolts migrate later than the sockeye salmon smolts, but the coho salmon smolts usually migrated during a period of relatively warmer water, when the abundance of migrating sockeye salmon smolts had greatly diminished. Similarly, Foerster and Ricker (1953) found that the coho salmon smolt migration in Cultus Lake and Sweltzer Creek, British Columbia, always followed the sockeye salmon smolt migration by about 10 days.

Although the seasonal timing of the outmigration of coho salmon smolts may vary from system to system, it is relatively consistent within a particular system. When time of migration is plotted against latitude, a definite south to north cline in time of migration becomes evident (Figure 8). Coho salmon smolts migrate later in the season in northerly systems than in more southerly ones. More than a month separates the midpoint of smolt migration from the central coast of California (lat 37° N) to the Gulf of Alaska (lat 60° N). This relation also applies for the Asiatic side of the Pacific Ocean.

DIEL PATTERN OF MIGRATION

The transformation of juvenile coho salmon from either lake- or stream-type residents to smolts is associated with avoidance of light and increasing nocturnal activity (Hoar, Keenleyside, and Goodall, 1957; Hoar, 1958; Smirnov, 1960).

Although most of the migration of smolts to salt water occurs during the darkest hours of the night, some occurs during the daytime. At Karluk Lake, for instance, during some years almost 40% of the coho salmon smolts migrated in the daytime—between 0600 and 1800 hr (Figure 9). In other coho salmon rivers, the percentage of smolts that migrate seaward during daylight is quite variable. In the Bolshaya River in Kamchatka, during the years 1944-47, 6.3 to 50.0% of the age 1 smolts[5] and 8.8 to 73.2%

TABLE 5.—Dates by which 50% of the coho and sockeye salmon smolts migrated from Karluk Lake, 1961-68.

Year	Sampling period	50% migration date	
		Coho salmon	Sockeye salmon
1961	May 25 to June 29	June 10	June 2
1962	May 17 to June 21	June 10	May 29
1963	May 18 to July 6	June 12	June 6
1964	May 17 to July 6	June 2	June 3
1965	May 16 to July 16	June 18	June 6
1966	May 18 to July 2	June 15	June 4
1967	May 18 to June 29	June 5	May 27
1968	May 17 to June 26	June 12	May 24

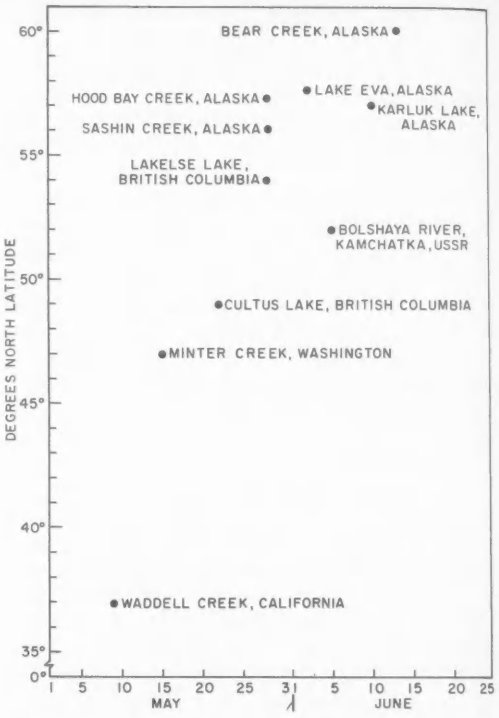

FIGURE 8.—Average date when 50% of the coho salmon smolts had migrated from river and lake systems along the Pacific coast of North America and Asia.

[5] Fish that go to sea in their second year.

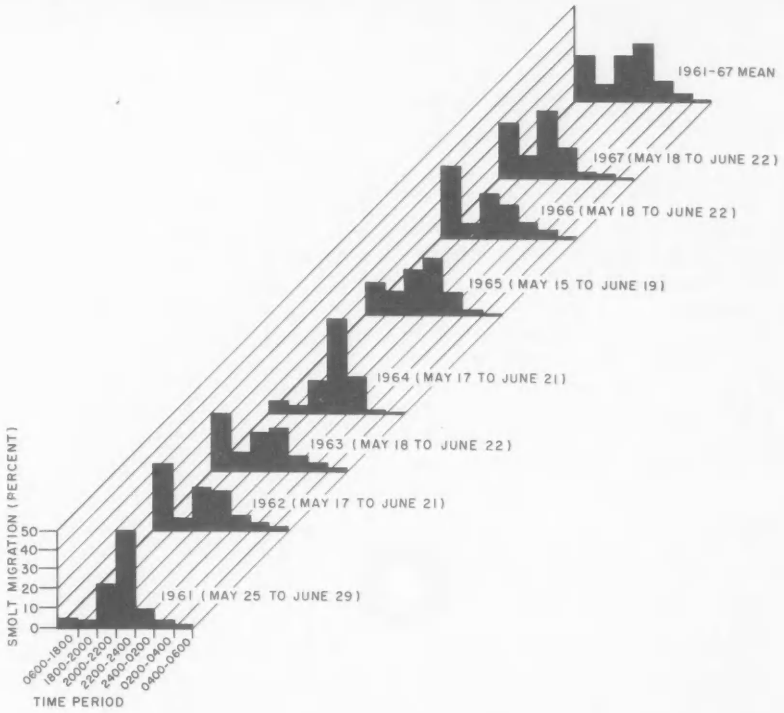

FIGURE 9.—Migration of coho salmon smolts by time period from Karluk Lake for the years 1961-67.

of the age 2 smolts migrated in daylight (Semko, 1954.) At Bear Creek, Alaska, 49.8% of the smolts migrated between 0400 and 2000 hr in 1962 (see footnote 1, Table 1), and 16% migrated between 0900 and 1700 hr in 1964 (see footnote 2, Table 3).

AGE

In 1956, 1965, and 1968, scale samples taken from seaward-migrating coho salmon smolts at the Karluk Lake weir revealed that the dominant ages were 2 and 3 and that the age composition was similar between years (Table 6).

The freshwater age composition determined from the scales of adults collected in 1966 was strikingly similar to the age composition of seaward-migrating smolts in 1965—smolts that produced the adults in 1966 (Table 6). The only group missing from the adult scale sample but present in small numbers in the smolt scale samples was age 1 (fish that went to sea in their second year of life). Fish from this age class could have been missing in the returning adults

TABLE 6.—Freshwater age composition of Karluk Lake coho salmon as determined from smolt and adult scale samples.

Freshwater age	Percent composition			
	From smolt scales			From adult scales
	1956	1965	1968	1966
1	1.4	3.0	3.0	—
2	44.5	51.5	48.5	56.9
3	49.1	43.9	42.5	41.7
4	4.9	1.5	6.0	1.4

because (1) they had poor ocean survival because of their small size; (2) the young overwintered in the river and migrated as age 2 smolts the following year; or (3) the young never migrated at all.

SIZE

Only lengths were measured in 1956, and lengths and weights were taken in 1965 and 1968. A summary of average size data by age class is presented in Table 7. Average lengths for comparable age classes were greater in 1968 than in 1956 and 1965. Average weights, with the exception of age 3 fish, were less in 1968 than 1965. Differences in lengths and weights between smolts for the two comparable years (1965 and 1968) are reflected in the condition factor (K), or coefficient of condition, which indicates the relative well-being of the fish. In 1965 all age groups had K values greater than 1.0000; the range was 1.0544 to 1.3695. In 1968 all K values were under 1.0000; the range was 0.9187 to 0.9600.

Information on the size of coho salmon smolts from other spawning systems is presented in Table 8. This table gives information for natural or "wild" populations and not for artificially hatched or reared stocks. Karluk Lake coho salmon smolts were generally as large as smolts of the same age from other areas or larger.

POSSIBLE EFFECTS OF INCREASED FRESHWATER RESIDENCE ON SURVIVAL OF COHO SALMON

The extended period of freshwater residence resulting in coho salmon smolts of age 3 occurs in many systems but seems to be significant only at Karluk.

It is interesting to hypothesize what effect a prolonged freshwater residence has on the annual return of adult coho salmon at Karluk Lake. Is an increased freshwater residence advantageous or disadvantageous to survival of each year class? What effect is there on marine survival of coho salmon if they take up ocean residence at an older age and consequently a larger size?

One means of answering these questions is to examine freshwater and marine survival rates for coho salmon from other areas. Survival from egg to smolt (fresh water) and smolt to returning adult (marine) are shown in Table 9 for some areas in California, Oregon, Washington, and British Columbia. Both freshwater and marine survival for age 1 smolts from these areas are quite variable: 0.13 to 12.00% and 3.77 to 11.79% respectively. The survival data in Table 9 pertain to stocks in which the smolts were primarily age 1 when they migrated to sea, and the application of these data to more northern stocks in which the smolts are mostly older and larger when they migrate must be done with caution.

The small population of age 2 smolts from Sweltzer Creek in British Columbia (Table 9) is of interest because these fish are more comparable to Karluk smolts, in that they may possibly have had a period of lake residence. Marine survival of these older, larger fish was high. Of 72 fin-clipped migrating age 2 smolts, 19 (26%) returned 5 or 6 months later as 3_3 fish (Foerster and Ricker, 1953). Although marine survival for these age 2 smolts might have been lower if they had spent another year in the ocean, it

TABLE 7.—Average length, weight, and condition factor of coho salmon smolts by age from Karluk Lake, 1956, 1965, and 1968.

Age	1956			1965			1968		
	Length	Weight	Condition factor	Length	Weight	Condition factor	Length	Weight	Condition factor
	mm	g		mm	g		mm	g	
1	106.8	--	--	112.5	19.5	1.3695	114.8	13.9	0.9187
2	139.7	--	--	136.3	28.2	1.0544	140.1	26.4	0.9600
3	151.1	--	--	141.7	30.7	1.0790	160.4	38.5	0.9329
4	165.4	--	--	177.0	63.9	1.1523	181.8	56.2	0.9353

TABLE 8.—Average fork lengths of coho salmon smolts of ages 1 to 4 from river and lake systems along the Pacific coast of North America and Asia, arranged geographically from north to south.

Area and year	Age				Reference
	1	2	3	4	
	mm	mm	mm	mm	
North America					
Hood Bay Creek, Alaska					
1968	83.0	96.0	--	--	Armstrong (1970)
1969	79.0	91.0	--	--	Armstrong (1970)
Karluk River (Karluk Lake), Alaska					
1956	106.8	139.7	151.1	165.4	Present study
1965	112.5	136.3	141.7	177.0	Present study
1968	114.8	140.1	160.4	181.8	Present study
Bear Creek, Alaska					
1962	106.3	118.7	150.8	--	Logan[1]
Sweltzer Creek (Cultus Lake), British Columbia					
--	110-120	--	--	--	Foerster and Ricker (1953)
1939	--	291.6	--	--	Foerster and Ricker (1953)
Minter Creek, Wash.					
1940	[2]96.3	--	--	--	Salo and Bayliff (1958)
1953	[2]99.7	--	--	--	Salo and Bayliff (1958)
Deer Creek, Oreg.					
1960	88.7	--	--	--	Chapman (1961)
Flynn Creek, Oreg.					
1960	88.1	--	--	--	Chapman (1961)
Waddell Creek, Calif.					
1933	113.5	--	--	--	Shapovalov and Taft (1954)
1934	113.3	--	--	--	Shapovalov and Taft (1954)
1935	113.1	--	--	--	Shapovalov and Taft (1954)
1936	116.6	--	--	--	Shapovalov and Taft (1954)
1937	114.8	--	--	--	Shapovalov and Taft (1954)
1938	112.4	--	--	--	Shapovalov and Taft (1954)
1939	112.4	--	--	--	Shapovalov and Taft (1954)
1940	109.5	--	--	--	Shapovalov and Taft (1954)
1941	103.1	--	--	--	Shapovalov and Taft (1954)
Asia					
Bolshaya River, Kamchatka, USSR					
--	85.0	130.0	--	--	Semko (1954)

[1] Personal communication, Sidney M. Logan, Fishery Biologist, Alaska Department of Fish and Game, May 3, 1967.
[2] Primarily age 1 fish.

TABLE 9.—Average freshwater and marine survival for coho salmon from various streams along the Pacific coast of North America, arranged geographically from north to south.

Streams	Percent survival		Reference
	Fresh water	Marine	
	Egg to age 1 smolt	Age 1 smolt to adult	
Nile Creek, British Columbia	1.40	6.00	Wickett (1951)
Hooknose Creek, British Columbia	1.30	11.79	Godfrey (1965)
Sweltzer Creek, British Columbia	[1]0.13	8.07	Foerster and Ricker (1953)
Sweltzer Creek, British Columbia	[2,3]0.33	--	Foerster and Ricker (1953)
Sweltzer Creek, British Columbia	--	[4]26.39	Foerster and Ricker (1953)
Minter Creek, Wash.	3.22	3.77	Salo and Bayliff (1958)
Deer Creek, Oreg.	12.00	--	Chapman (1961)
Waddell Creek, Calif.	1.35	4.95	Shapovalov and Taft (1954)

[1] Before piscivorous fishes were controlled.
[2] After piscivorous fishes were controlled.
[3] Geometric mean.
[4] Age 2 fish only.

nevertheless was considerably higher than for any of the age 1 smolts.

In the absence of knowledge of survival rates for the more northern populations of coho salmon, an examination of the effect of increased freshwater residence on sockeye salmon, the dominant species of salmon in the Karluk system, is of value. Sockeye salmon juveniles at Karluk Lake have long been known to reside in the lake a year or more longer than do sockeye salmon in other areas (Gilbert and Rich, 1927). In most Alaska systems, sockeye salmon smolts migrate at the beginning of their second or third year of life, but at Karluk Lake most sockeye salmon smolts migrate at the beginning of their third or fourth years. Possibly the factor(s) responsible for the 1-year holdover of juvenile sockeye salmon in the lake may also be responsible for the holdover of juvenile coho salmon.

Freshwater survival of sockeye salmon at Karluk Lake is extremely poor, but marine survival is good. During the late 1920's and early 1930's, freshwater survival was less than 1% and ocean survival was about 21% (Barnaby, 1944). In recent years, freshwater survival has dropped to less than 0.5% and ocean survival has increased to about 40%.[6] Ricker (1962) modified Barnaby's data by applying a marking mortality factor derived from his Cultus Lake studies and determined that the older, larger smolts have greater marine survival and that Barnaby's original estimate of 21% survival was too low. Average marine survival by freshwater age for the years 1926 and 1929-33 were as follows: age 1 smolts, 18.3%; age 2, 27.4%; age 3, 34.2%, and age 4, 33.3%. Ricker attributed the high ocean survival to the large size of the smolts when they entered salt water. The larger size of the sockeye salmon smolts at the time of seaward migration, however, is offset by a greater total freshwater mortality due to their prolonged stay in the lake.

I have shown that in the more northern latitudes coho salmon usually reside a minimum of one extra year in fresh water before they migrate to sea. Generally, a longer period of freshwater residence will result in greater freshwater mortality but lower marine mortality because the fish are larger when they enter the ocean. Most likely, as with Karluk Lake juvenile sockeye salmon, an extra year in the lake for juvenile coho salmon probably results in a greater total freshwater mortality. Total marine mortality, however, may be less for coho salmon than for sockeye salmon because the coho salmon generally spend less time at sea before returning to spawn (12 to 18 months rather than 24 to 30 months).

SUMMARY AND CONCLUSIONS

Both the freshwater and total ages of adult coho salmon increase from southern to northern latitudes. In California, the southern portion of the coho salmon's range, fish of ages 3_2 and 2_2 are in the majority, but in the northern areas, ages 4_3 and 3_2 predominate. Karluk coho salmon, however, are unique, in that although age 4_3 fish are still the primary age class, the age 3_2 fish are replaced by age 5_4, so that age 5_4 fish account for 42% of the run. In no other North American or Asiatic coho salmon stock for which information is available is such a large percentage of the run composed of 5_4 fish.

The increase in total age of coho salmon from south to north is associated with the increased time the juveniles spend in fresh water. The small numbers of age 5_4 fish in several Alaska stocks may represent juveniles that live in lakes rather than rivers.

Fecundity generally increases from south to north, and Karluk coho salmon are the most fecund of any North American stock and closely parallel the highly fecund Asiatic stocks from the Kamchatka Peninsula. In Karluk coho salmon, there is a relation between number of eggs and length but no relation between egg size and length or egg size and fecundity. Egg counts are significantly higher in the right ovary than in the left.

Coho salmon smolts generally migrate after the ice breaks up and the water warms. In North America, the migration is earlier in southern latitudes than northern ones. The coho salmon

[6] Unpublished data on file at National Marine Fisheries Service Auke Bay Fisheries Laboratory, Auke Bay, Alaska 99821.

migration at Karluk Lake is primarily nocturnal, although some daytime migration does occur.

A prolonged freshwater residence by juvenile coho salmon in Karluk Lake should result in a greater total freshwater mortality, but the resulting larger smolts should have a lower total marine mortality. Coho salmon at Karluk may have an even lower marine mortality than sockeye salmon, in part because the coho salmon spend less time at sea.

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DEVELOPMENTAL RATES AT VARIOUS TEMPERATURES OF EMBRYOS OF THE NORTHERN LOBSTER (*Homarus americanus* MILNE-EDWARDS)

HERBERT C. PERKINS[1]

ABSTRACT

The rates of development, time from extrusion to hatching at various temperatures, and differential developmental rates at the same temperature of lobster embryos are presented. The eyes of the embryos were measured to monitor the rates and degree of embryo development.

Herrick (1890, 1896) discussed developmental rates for lobster embryos in the early stages at 20° to 22° C. Templeman (1940) determined the times required at various temperatures for lobster eggs to reach the 16-cell stage, and up to the formation of eye pigment. The information from these studies is valuable for determining the rates of early development in lobster egg-embryos but is not adequate for the accurate assessment of developing embryos once eye pigment has been formed. By monitoring the rate of development of lobster embryos throughout the embryonic period at various temperatures one can predict hatching times of larvae and control hatching times by manipulating the water temperature in tanks holding egg-bearing females, so that larvae can be available over a wide period of time for use in experiments. This paper presents the rates of development and time required to complete the embryonic period by lobster embryos at various temperatures and a method of continually monitoring that development. The work was conducted at the National Marine Fisheries Service, Biological Laboratory, Boothbay Harbor, Maine, as part of the Laboratory's investigation of the early life history of the lobster.

METHODS AND MATERIALS

Most of the egg-bearing lobsters used in this study came from the offshore canyons of the continental shelf, south and east of New England. A few came from the Boothbay Harbor area and are so noted. All egg-bearing females were kept in tanks at seasonal water temperatures or in water warmed to various constant temperatures. Water from the laboratory's seawater system was piped to the heated tanks at rates consistent with the capacity of the heaters. Salinity averaged 31‰ and ranged from 29 to 32‰ throughout the study period.

Five egg-bearing females were kept in a tank through which natural seawater at seasonal temperature was circulated during the developmental period of their eggs. The purpose of holding these females at seasonal temperatures was to determine the rates of development of their embryos in a natural temperature regime. Fourteen female lobsters from the offshore canyons, with recently extruded eggs (eggs in prenaupliar condition), were kept at constant temperatures from 6.9° to 24.6° C. The primary objective at the higher temperatures (20°-24.6° C) was to force the eggs to hatch before the time they would do so at seasonal temperatures. Of further interest was the rate of development of the embryos at constant, rather than fluctuating, temperatures, and the time required for the eggs to hatch at these temperatures from a given point in their development.

The rates and extent of development of the embryos were determined by measuring the size of their eyes. Measurements were made to the nearest micron with an ocular micrometer in a dissecting microscope at a magnification of 50×. When measuring an eye, I took its greatest width and greatest length, combined these figures and

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divided by two. The resulting figure was used as an index of development only and was not meant to represent the actual increase or growth of the eye. Samples of 15 to 20 eggs were removed from the periphery of an egg mass whenever a measurement was desired (usually once a week). From these samples five eggs were selected randomly, and one eye of each embryo measured. A mean of these five measurements was used as a working figure or index. Eggs were taken from the peripheral layer of the mass as these are the furthest advanced in development and are the first to hatch. Variation in the eye measurements of eggs from this layer ranges from zero to 5%. When the eyes first appear and are large enough to measure, they are but thin crescents, darkly pigmented and surrounded by a halo of lighter material. The dark crescents only were measured. The eyes are very distinct for most of the developmental period and are easily measured, the crescents gradually becoming tear-drop in shape. The index of the eye is about 70μ when it is first measurable; the index is about 560μ at hatching. All eyes were measured after the eggs had been preserved in a 5% solution of Formalin in seawater. Preservation in Formalin caused significant swelling in the eggs themselves but had no determinable effect on the size of the eyes.

RESULTS AND DISCUSSION

TRENDS OF EMBRYONIC DEVELOPMENT IN WATER OF SEASONAL TEMPERATURES

The developmental patterns, from onset of eye pigment to hatching, of the embryos of the five females held at seasonal temperatures are shown in Figure 1, as is the cycle of water temperature for the same period. The trends of embryonic development were plotted by using periodic (usually weekly) measurements of the eye index of each egg mass. These five lobsters had extruded their eggs in the laboratory tanks so the age of each egg mass was known. From the latter part of November to the first of May of the following year, water temperatures were no higher than 6° C. Embryonic development during this period ceased in some of the egg masses and was barely discernible in others, at least by the method of eye index measurement. Squires (1970), using the amount of yolk material in the eggs as a criterion, reported a standstill in development during the winter in embryos of Newfoundland lobsters.

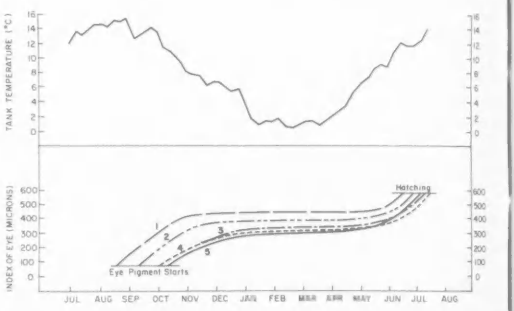

FIGURE 1.—Trends of development of the embryos of five female lobsters held in water of seasonal temperature at the Boothbay Harbor Laboratory and the temperature cycle during the period. The lines showing developmental trends are derived from plots of periodic measurements of the embryos' eye indices. The lines are numbered in accordance with the age of the egg mass; the lower the number, the older the egg mass.

DIFFERENTIAL RATES OF DEVELOPMENT

The developmental rates of lobster embryos appear to be governed not only by their thermal environment, but by the age or extent of development at which they are subjected to that environment. During the experiments I conducted the older or more advanced embryos developed at slower rates than those less advanced, though all were maintained in the same tank. The oldest egg mass of the five females held under seasonal conditions was extruded 7 weeks before the youngest, but the total time for development of the younger egg mass was 4½ weeks less than the older; the younger embryos had developed considerably faster. Measurements of the eye index of embryos in all five egg masses were made for the first time on November 7. In Fig-

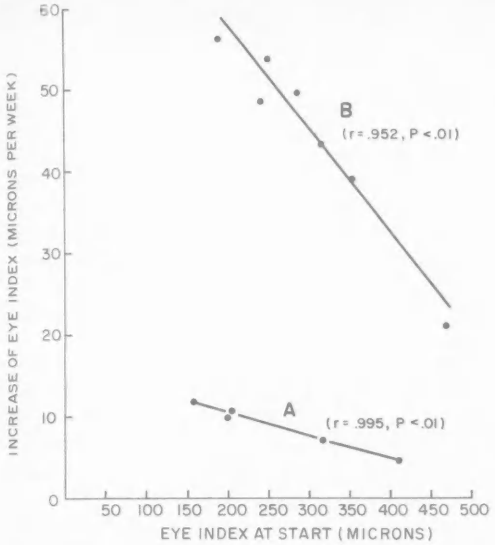

FIGURE 2.—Line A represents the different rates of increase of the eye index, in microns per week, of the embryos of the five lobsters held in the same tank, under seasonal conditions, from November 7, until hatching. Line B represents the different rates of eye increase of the embryos of seven females held at a constant temperature of 22.6° C. Size of eye index at the starting time is plotted against the corresponding rate of increase of the eye index up to the time of hatching.

TABLE 1.—Lobster number, carapace length of female, age of eggs 10 January, increase of eye index of embryos from 10 January to 26 March, and the total developmental time for the embryos of the five female lobsters held under seasonal water conditions at the Boothbay Harbor Laboratory.

Lobster number	Carapace length (mm)	Area of capture	Age of eggs 10 January (weeks)	Increase of eye index (microns/week) 10 Jan.-26 Mar.	Total weeks to hatching
1	97	Boothbay Harbor	29	0.00	51.4
2	94	Boothbay Harbor	26	0.46	50.6
3	147	Veatch Canyon	24	0.65	50.0
4	124	Hudson Canyon	23	1.49	49.4
5	94	Boothbay Harbor	22	2.52	47.0

surable increase in development during this time, whereas some development was noted in the embryos of the other egg masses. In fact, the embryos in the oldest egg mass showed no measurable increase from the second week of December to the middle of the following April. The number of weeks during the winter in which no development could be measured, for each egg mass, was as follows (as in Table 1, lobsters are numbered according to the age of their egg mass):

Lobster number	*Number of "dormant" weeks during winter*
1	18
2	14
3	8
4	6
5	0

ure 2(A) the rate of eye increase (microns per week) of the embryos in each egg mass for the remainder of the developmental period is plotted against the corresponding eye index taken on November 7. The same result is obtained if the age of an egg mass is substituted for its eye index on the abscissa. Rates of increase were calculated by dividing the total increase of the eye index by the total number of weeks the embryos took to complete development after November 7. The increase in eye index (microns per week) of embryos in each egg mass, for the period January 10 to March 26, is presented in Table 1. During this time the water temperature ranged between 0.1° and 1.5° C; the mean was 1.0°. This was the coldest 10-week interval of the developmental period. The embryos in the oldest egg mass exhibited no noticeable or mea-

The rates of increase (microns per week) in eye index for the embryos of seven lobsters held at a constant temperature of 22.6° C are indicated in Figure 2(B). These females came from offshore canyons of the continental shelf, off New England. The ages of these egg masses were not known, but the eye index of the embryos in each was measured before the females were placed in the warm water. The increase in eye index of the embryos in each egg mass was monitored weekly until hatching. Times and rates pertain only to the time spent at 22.6° C. Although one might expect that in a given time interval, at the same temperatures, younger embryos would develop faster than older ones, it might also be expected that the younger embryos would assume the slower growth rate of the older when they eventually reached the same age. Of

the five females held in water of seasonal temperature, the youngest eggs were at lower temperatures than the older at the same age, making assessment of differential developmental rate difficult. However, of the seven egg masses held at 22.6° C the embryos of least development at the start developed faster at comparable levels of development than the more advanced embryos. The differential rate of development of lobster embryos, at the same temperature, seems to imply that in a given population where extrusion of eggs may be somewhat staggered in time among the females, hatching of the eggs would occur during a more limited period, providing the egg-bearing females occupied the same thermal environment.

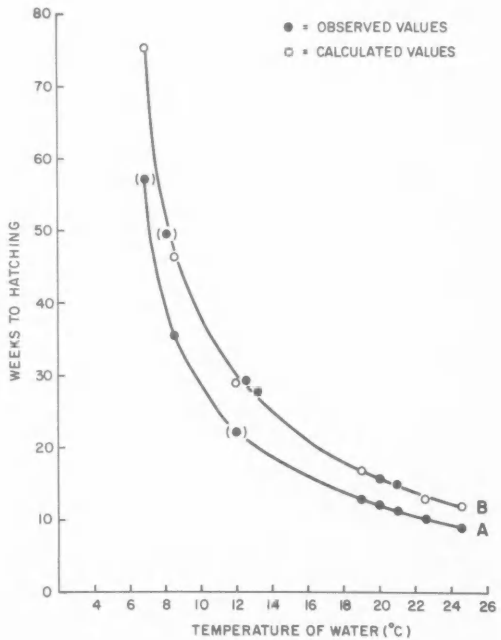

FIGURE 3.—The number of weeks for lobster eggs to complete the embryonic period at various temperatures. Line A represents the time required from onset of eye pigment in the embryos; line B represents the time required from extrusion to hatching. Points in parentheses indicate times required at the mean temperature of a fluctuating thermal environment.

RATES OF DEVELOPMENT AT VARIOUS TEMPERATURES

The times required for the embryos to hatch at various temperatures are shown in Figure 3. Line A represents the time required for the embryos to hatch after the formation of eye pigment; line B represents the time required from extrusion to hatching. Most of the points in each line indicate the time required to complete development at constant temperatures. A few (points in parentheses), representing the time required for total development at the mean temperature of a fluctuating thermal environment, have been included as well. For example, the average time required for total development of the eggs of the five females held under seasonal conditions was 49.7 weeks. The mean water temperature during the period was 8.1° C. These values are virtually the same as would be expected if the water was held constantly at 8° C.

All values showing time from onset of eye pigment to hatching were observed. The times required from extrusion to hatching at five temperatures were also observed. To find the unknown time required from extrusion to hatching, at other temperatures, I used the following equation:

$$\frac{A_1}{X_1} = \frac{A_2}{X_2}$$

where A_1 was the observed time from onset of eye pigment to hatching at 20° C; A_2 was the observed time from extrusion to hatching at 20° C; X_1 was the observed time required from

TABLE 2.—Number of weeks required from extrusion to onset of eye pigment, onset of eye pigment to hatching, and to hatching at certain temperatures, at salinities near 31‰.

Water temperature (° C)	Weeks required from		
	Extrusion to onset of eye pigment	Onset of eye pigment to hatching	Extrusion to hatching
5	40	120	160
10	9	30	39
15	5	18	23
20	4	12	16
25	3	9	12

onset of eye pigment to hatching at a given temperature; and X_2 is the unknown time required from extrusion to hatching at the same temperature as X_1. Templeman (1940, p. 74) used a similar method to find unknown developmental rates. The requisite times for development of lobster embryos at certain temperatures are summarized in Table 2. The relationship between water temperature and the average increase in eye index of lobster embryos, in microns per week, is linear at temperatures between 5° and 25° C. The index of the embryonic eye must increase to approximately 560μ at hatching. If eggs are encountered with eyed embryos, their eye index may be subtracted from 560 and the difference divided by the value calculated from the following equation:

$$\hat{Y} = -8.3151 + 2.6019(X)$$

where Y is the increase of the eye index in microns per week, and X is the developmental temperature. The resulting quotient is the average number of remaining weeks required for the embryos to hatch, depending on genetic variation and the differential rate of development noted earlier.

SUMMARY

1. Once eye pigment has been formed, the course and rate of development of lobster embryos may be monitored by the periodic measuring of the eye of the embryos.

2. Lobster embryos develop differentially, under the same thermal conditions, depending on their age or extent of development when they are subjected to a given thermal environment.

3. As water temperature has a direct effect on the developmental rate of lobster embryos, that rate may be manipulated by adjusting the water temperature of holding tanks to insure periodic hatches of larvae throughout the year.

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PRELIMINARY STUDIES OF SELECTED ENVIRONMENTAL AND NUTRITIONAL REQUIREMENTS FOR THE CULTURE OF PENAEID SHRIMP[1]

LOWELL V. SICK, JAMES W. ANDREWS, AND DAVID B. WHITE[2]

ABSTRACT

Types of substrate, type of aeration, and stocking density were compared as prerequisities for high-density culture studies with penaeid shrimps. Neither sand-shell substrate nor brick subdivisions of culture tank bottoms produced significantly higher survival rates than bare fiber glass tanks. Forced air supplied via airstones proved to be a more suitable form of aeration than did physical agitation of the water column in culture tanks by high-pressure nozzles. Survival rates of 80 to 90% were achieved when biomass densities did not exceed 40 g/m^2.

Semipurified pelleted diets (i.e., containing defined chemical ingredients plus one or more natural products) having a complement of nutrients including minerals and vitamins, various ratios of shrimp to fish meal, protein hydrolysates, and such diets fed at three percentages of total biomass daily were compared for their ability to produce increases in growth. Diets without fish or shrimp meal sustained biomass while those diets having the highest proportion of shrimp to fish meal in addition to added vitamins produced over 60% increase in total biomass over a 3-month period. Animals fed a combination of yeast, soy, and casein hydrolysates increased 39% in biomass over the same period of time while those fed each of the above hydrolysates during the 3-month period separately showed only an average of 18% increase in weight. Feeding shrimp with a fish-shrimp base with added vitamins at a rate of 15% daily of the total biomass produced a 164% increase in weight with 95 to 100% survival during the 3-month period. Using semipurified pelleted diets, a food conversion ratio of 5.5 was obtained.

Establishing selected preliminary environmental and nutritional requirements for penaeid shrimp resulted in the successful and reproducible production of major biomass increases with relatively high survival rates and low food conversion ratios.

The harvest of commercial shrimp suffers great seasonal variability and has failed to keep pace with ever-increasing domestic and export demands (Surdi and Whitaker, 1971). In order to supplement the natural harvest and provide a year-round supply of shrimp, several attempts have been made to culture shrimp in natural ponds, restricted portions of bays and estuaries, and laboratory tanks. In general, these efforts have had limited success and have explicitly illustrated the need for more accurately defining the nutritional and environmental requirements necessary for culturing these species. Although pond culture has produced annual crops of shrimps (Villadolid and Villaluz, 1951; Lunz, 1967; Wheeler, 1967; Broom, 1969; Moore and Elan, 1970[3]), production has been minimal and highly variable. Attempts to obtain commercial quantities of shrimp by stocking enclosed portions of estuaries have to date not yielded production results (American Fish Farmer & World Aquaculture News, 1970). During recent laboratory studies, Subrahmanyam and Oppenheimer (1969) were able to maintain shrimp in laboratory tanks using a pelleted diet consisting of fish meal, stickwater, and vitamins. However, the

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[3] Moore, W. R., and L. L. Elan. 1970. Salt water pond research. Tex. Parks Wildl. Dep., Austin. (Processed.)

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total biomass increase of shrimp fed their best diet for 6 weeks was only approximately 50% higher than initial biomass. Better results (on an individual weight basis) using *Penaeus duorarum* were obtained from animals grown on a sand substrate than those grown in bare tanks.

The greatest promise for economical shrimp production lies in determining the exact nutritional requirements and developing an inexpensive artificial diet from feedstuffs for these species. Current commercial practices in Japan employ chopped clam (predominantly *Tapes semidecussata*, Reeve) as a diet for rearing shrimp. Despite the high market price for cultured shrimp in Japan (the retail price of cultured shrimp ranged from $4 to $10 per pound in 1970), shrimp farming there tends to be a marginal enterprise because of the high cost of a clam diet. However, in other parts of the world where shrimp does not command such a luxury price, the use of a high-value product such as clam for shrimp feed is prohibited.

Pelleted diets (i.e., pellets containing all the chemical ingredients thought to be important to animal growth) have been designed consisting of purified soybean meal, glucose, sucrose, starch, glucosamine, chitin, cellulose, soybean oil, citric acid, succinic acid, amino acid, minerals, vitamins, and cholesterol (Kanazawa et al., 1970). After growing penaeids on such diets, the animals were in excellent physiological condition, but in the best group, total biomass increase was only 72% of the control group fed chopped clam. Thus, little progress has been made toward establishing nutritional and environmental requirements that will yield optimum growth (total biomass increase) and survival of penaeid shrimp.

In the present study, an attempt was made to develop a suitable experimental culture system which could serve as a model for future nutritional and environmental studies. Several environmental factors were examined, and, as a result, environmental conditions were created which would allow acceptable growth and survival. Having first established suitable culture conditions, several diets were evaluated in preliminary studies of the nutritional requirements of shrimp.

MATERIALS AND METHODS

Both environmental and nutritional studies were conducted in round fiber glass culture tanks measuring approximately 1 m deep by 1 m in diameter and equipped with a venturi type center drain which maintained a water depth of 0.75 m. Three replicates were maintained for all treatments.

Water (ranging in salinity from 26.8 to 29.3‰) from the Skidaway River was filtered through an oyster shell and sand filter to remove major food particles. Filtered water was heated to 30° C in a stainless steel heat exchanger and jetted into each tank at a rate of 1.9 liters/min through flow-control nozzles which were aimed so that the agitation of the water column in each tank was minimal. Temperature ranged from 25° to 28°C in each tank throughout the experimental period.

White shrimp (*P. setiferus*) obtained from the Savannah, Ga., river and tributary systems were used in all environmental experiments, and brown shrimp (*P. aztecus*) obtained from the Tampa Bay, Fla., area were used in the nutritional studies. Shrimp weighing 4 ± 0.8 g (mean and standard deviation based on 480 weighed shrimp) were selected from the above stock and used in all environmental studies (10 animals per tank) and fed pelleted diets (Table 1, Diet 1) at a rate of 5% of their biomass daily, on a dry weight basis. Shrimp were weighed each week and the percent increase or loss recorded on a wet weight basis.

SUBSTRATE STUDY

Sand-shell substrates suitable for burrowing, subdivisions of tank bottoms, and bare fiber glass tank bottoms were provided for replicate groups of shrimp, and relative survival rates among the treatment groups were compared over a 5-week period. Sand-shell substrates were placed directly onto the tank bottom in one group, and in another group, the same substrate was placed on a perforated platform 10 cm above the tank bottom, allowing a flow of water through the drain below the sand surface. Such an arrangement was designed to test the effect of decreasing the

TABLE 1.—Experimental variables and results from four nutritional studies with penaeid shrimp.

	Group I, Diets				Group II, Diets					Group III, Diets				Group IV, Diets			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Casein (%)	50.2	50.2	50.2	--	28.5	8.0	28.5	23.5	--	--	--	--	--	--	8.0	8.0	8.0	--
Methionine (%)	1.0	1.0	1.0	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Glycine (%)	0.1	0.1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Sodium glutamate (%)	0.2	0.2	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Citric acid (%)	0.3	0.3	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Succinic acid (%)	0.3	0.3	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Mineral mix[1] (%)	5.0	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Fat[2] (%)	8.0	8.0	8.0	--	8.0	8.0	--	8.0	--	8.0	8.0	8.0	8.0	--	8.0	8.0	8.0	--
Carbohydrate premix[3] (%)	20.5	20.5	20.5	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Shrimp meal (%)	--	--	--	--	28.5	69.5	36.5	23.5	--	28.5	28.5	28.5	28.5	--	69.5	69.5	69.5	--
Anchovy meal (%)	--	--	--	--	28.5	8.0	28.5	23.5	--	28.5	28.5	28.5	28.5	--	8.0	8.0	8.0	--
Shrimp muscle (%)	--	--	--	--	--	--	--	15.0	--	--	--	--	--	--	--	--	--	--
Yeast protein hydrolysate[4] (%)	--	--	--	--	--	--	--	--	--	24.5	--	--	8.1	--	--	--	--	--
Casein protein hydrolysate[4] (%)	--	--	--	--	--	--	--	--	--	--	24.5	--	8.1	--	--	--	--	--
Soy protein hydroysate[4] (%)	--	--	--	--	--	--	--	--	--	--	--	24.5	8.1	--	--	--	--	--
Collagen (%)	4.0	4.0	4.0	--	4.0	4.0	4.0	10.0	--	8.0	8.0	8.0	8.0	--	4.0	4.0	4.0	--
Vitamin mix[5] (%)	2.5	2.5	2.5	--	2.5	2.5	2.5	2.5	--	2.5	2.5	2.5	2.5	--	2.5	2.5	2.5	--
Cellulose (%)	7.9	12.9	13.8	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Daily feeding rate (% of biomass)	5	5	5	0	5	5	5	5	0	5	5	5	5	0	5	10	15	0
Duration (weeks)	5	11	11	11	11	11	11	11	11	6	6	6	6	6	6	6	6	6
Results:																		
% increase in biomass	18	0	0	0	44	63	50	37	--	19	18	18	39	--	58	109	164	--
Survival rate (%)	80	80	80	0	90	100	90	80	0	90	80	80	90	27	80	90	90	26

[1] Contains 30.0% KH_2PO_4, 9.4% KCl, 14.8% $MgSO_4$, 27.4% $CaHPO_4 \cdot 2H_2O$, 1.4% $FeCl_3$, 0.2% $MnSO_4 \cdot 7H_2O$, and 16.8% $CaCO_3$.
[2] Contains 33⅓% corn oil, 33⅓% hydrolyzed vegetable and animal fat, and 33⅓% menhaden oil.
[3] Contains 24.3% corn starch, 24.3% sucrose, 24.3% glucose, 19.5% chitin, and 7.6% glucosamine.
[4] Nutritional Biochemical Co. enzymatic hydrolysates.
[5] Nutritional Biochemical Co., Cleveland, Ohio, standard vitamin diet fortification mixture in dextrose.

buildup of anaerobic conditions. Division of tank bottoms into sundry tunnels and levels was created by specific placement of bricks and clay drain tiles.

AERATION STUDY

Aeration provided by jetting streams of filtered seawater into respective tanks was compared to aeration supplied by bubbling air through airstones into tanks in which water was continuously added with no agitation of the water column for an 8-week period. Two airstones were placed in each tank and valve-regulated air lines controlled the pressure at approximately 4 psi. Oxygen levels were monitored periodically and used along with survival rates as a basis for evaluation of replicate groups aerated by each method.

STOCKING DENSITY STUDY

Survival data were compared among triplicate tanks stocked at 10, 20, and 40 shrimp per m^2 for an 8-week period. These densities of approximately 40, 80, and 160 g/m^2 were chosen on the basis of data provided in pond and laboratory culture of penaeid shrimp (Broom, 1969; *Subrahmanyam and Oppenheimer, 1969*).

PRELIMINARY NUTRITIONAL STUDY

Triplicate groups of ten 4 g brown shrimp (*P. aztecus*) were fed a series of pelleted diets. Growth data (biomass increase) was used as a means of evaluation. Diets examined consisted of those patterned after Japanese purified diets (i.e., diets containing only chemical ingredients) (Table 1, Group I) (Diet 1 was conducted for 5 *weeks and Diets 2, 3, and 4 for 11 weeks each);* a second group of semipurified diets (i.e., con*taining defined chemical ingredients but contain*ing one or more natural products) providing four combinations of levels of protein, fat, shrimp, and fish meal (Group II) (conducted for 11 weeks); and a third group designed to compare the nutritional value of casein, yeast, and soy hydrolysates (Group III) (conducted for 6 weeks). All of these groups were fed at 5% of their respective biomass daily. In addition, Diet 6 was fed at 5, 10, and 15% of biomass (Group IV) (conducted for 6 weeks).

TABLE 2.—Percent of pellet dissolved over time and at at three concentrations of binder. (Values are means and standard deviation on two replicates with Diet 1.)

Percent binder (collagen) added	Hours		
	6	12	24
1			
3	13 ± 1.2	14 ± 0.9	18 ± 1.7
5	11 ± 0.8	10 ± 0.6	10 ± 0.6
10	10 ± 0.6	10 ± 1.1	10 ± 1.0

Combined environmental factors which produced best survival in each of the environmental experiments (i.e., culture conditions consisting of bare fiber glass tank bottoms, supplied aeration, and a stocking density of approximately 40 g/m^2) were used in all nutritional studies. This combination offered a maximum potential for an increase in biomass and therefore allowed accurate evaluation of differences among diets tested. Although survival in bare fiber glass tanks was not significantly different from sand substrates, the fact that bare tanks were simpler to maintain dictated that they be used for the nutritional studies.

Prior to starting nutritional studies, the physical properties of pelleted diets were evaluated for acceptability as shrimp food. Pellet consistency was determined according to its ability to resist dissolution over a given period of time, and texture and size were chosen according to animal performance when presented several choices. Collagen[4] proved to be a suitable binding agent. Using an experimental design with time and collagen levels as variables, a pellet with 5% collagen added as a binder was found to offer optimum consistency over a 24-hr immersion in salt water (Table 2). Percent dissolution was measured by taking dry weights after 6, 12, and 24 hr of immersion (no shattering of pellets was observed, and all loss of weight was therefore assumed to be from dissolution). Animals were observed to feed most readily on

[4] Supplied on an experimental basis by the Hides and Leather Division of the U.S. Department of Agriculture Eastern Utilization Laboratory in Philadelphia, Pa.

pellets 0.3 cm in diameter by approximately 1.5 cm in length and which sink in water, and hence, pellets having these characteristics were used in both environmental and nutritional experiments.

RESULTS AND DISCUSSION

SUBSTRATE STUDY

A survival rate of 80% was obtained after 5 weeks in tanks without substrate. 80 to 90% survival was maintained over much of the duration of the experiment among both treatments having sand-shell substrates, and less than 60% survival occurred among tanks having brick subdivisions (Figure 1). Although *P. setiferus* is reported to burrow less than either *P. duorarum* or *P. aztecus* (Anderson, 1966; Pérez Farfante, 1969), it apparently was able to avoid predation, especially during the highly vulnerable moulting period, quite successfully with or without a sand substrate, since 5-week survival data among the two sand-shell treatments and the bare tank bottom treatment were not significantly different ($P < 0.05$) (Duncan, 1955). If the type of shelter is a factor in increased survival for *penaeids maintained under culture conditions*, the brick subdivisions should have enhanced survival. However, the markedly high mortality rate among this group, significantly different from the other three treatments ($P < 0.05$), may have resulted from either failure of the shrimp to behaviorally segregate and thus fully utilize this protection or from physical abrasion against the sharp and coarse brick surface. Although there may have been toxic substances in the brick materials, the bricks were carefully washed and assumed to be otherwise inert in any chemical effect they may have had on the animals. Although differences in volume of water caused by placing various substrates in their respective treatments was not controlled for, it was felt that these differences in a running water system were not critical to the survival of shrimp. Differences in bottom area among the treatments caused by placement of different types of substrate were neither controlled for nor measured but were also thought to be negligible compared to differences found among treatment groups. The high degree of cannibalism noted by Subrahmanyam and Oppenheimer (1969) in tanks without substrate was not observed in any groups.

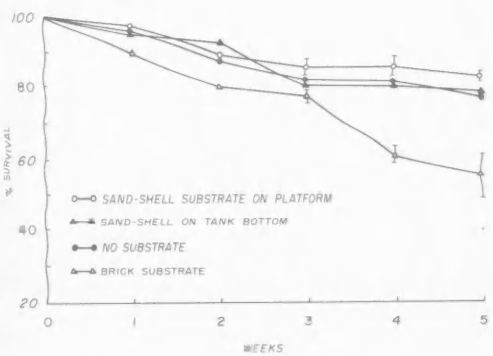

FIGURE 1.—Mean and standard error for percentage of animals surviving after 5 weeks of growth on four different substrates.

AERATION STUDY

The group having oxygen supplied by injecting air through airstones had significantly higher survival rates ($P < 0.05$) when compared with a treatment aerated by agitation of the water column (Figure 2). Although the average oxygen levels were similar between the two treatments (3.4-6.8 ppm), such levels in tanks aerated by high-pressure nozzles often dropped for short intervals due to clogging of the nozzles with silt and biological debris. Electrical power failures which affected water flow but not the compressed air supply (equipped with stand-by DC power) also caused intermittent drops in oxygen levels. Such short-term irregularities may have been more critical to shrimp tolerances than is indicated from reference to average oxygen level values, per se. Also, at the relatively high temperatures maintained throughout the study, short drops in oxygen levels could have been very critical. Decreased survival in tanks with agitation of the 0.75-m water column may also have resulted from physical agitation of the animals.

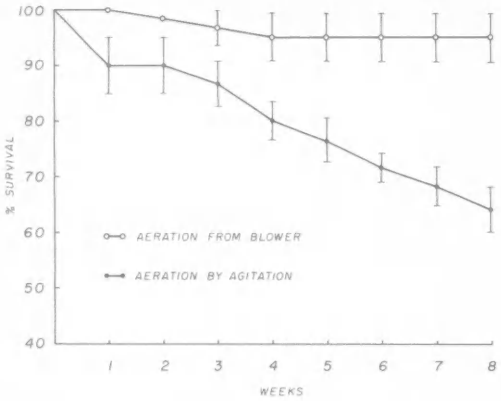

FIGURE 2.—Mean and standard error for percentage of animals surviving after 8 weeks of growth with two types of aeration.

STOCKING DENSITY STUDY

Stocking densities higher than 40 g/m² produced proportionally higher mortalities indicating an approximate carrying capacity for this particular culture system (Figure 3). If shrimp were stocked at 40 g/m², a population of 32 g/m² remained after 8 weeks. Similarly, when shrimp were stocked at 80 g/m², a relatively stable population of approximately 52 g/m² existed during the final 2 weeks of study. Similarly, mortality during the first 8 weeks among a population originally stocked at 160 g/m² created a population of approximately 80 g/m², but in this case the survival rate was still declining after 8 weeks of growth. Therefore, a carrying capacity (maximum biomass obtainable) for this culture system may have been somewhere between 32 and 80 g/m².

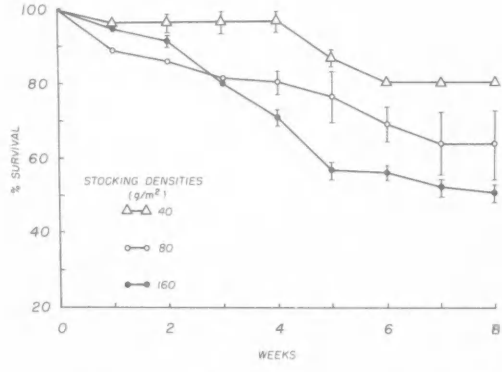

FIGURE 3.—Mean and standard error for percentage of animals surviving after 8 weeks of growth at three stocking densities.

Although such a carrying capacity would depend on the particular culture system, applicable calculations, utilizing data from a laboratory culture study (Subrahmanyam and Oppenheimer, 1969) and a pond culture experiment (Broom, 1969), indicate a similar carrying capacity for populations of other systems (ponds, embayments, and laboratory tanks). In the case of the laboratory study, best survival was obtained when shrimp were stocked initially at 34 g/m², yielding a biomass of 27 g/m² at the termination of the experiment. Likewise, best survival and an increase in biomass occurred in the pond culture study when initial stocking densities were below 20 to 30 g/m². Recent data from a commercial operator in Central America indicates that, regardless of stocked biomass, the carrying capacity ranged from 5.5 to 7.3 g/m² (Smitherman and Moss, 1970). Such evidence suggested that final production expectations should be considered in choosing initial stocking densities.

PRELIMINARY NUTRITIONAL EXPERIMENTS

A comparison of several groups of diets (Table 1) revealed that semipurified diets with casein as the major source of protein (Group I), only produced an average of 18% increase in biomass above stocked biomass levels. Group II, having fish and shrimp meal as additional sources of protein, produced approximately 63% growth on the best diet. Group III diets comparing hydrolyzed proteins yielded only 39% growth on the best diet, and animals fed at a rate of 15% of their total biomass (Group IV) increased their initial biomass 164%. In addition to increased

growth above that obtained in the environmental studies, survival was increased from 80 to 90% to 90 to 100% through the information acquired from the above nutritional comparisons.

Shrimp obtained little if any sustenance from organic or settled detritus since the continuous flow of filtered seawater through the tanks kept the system relatively free of siltation and extraneous growth. Furthermore, starved animals were not able to sustain their initial biomass level beyond 2 weeks, and the populations in all three replicate tanks had died after 7 weeks. Cannibalism appeared to be prevalent among starved organisms, and the decline in weight was undoubtedly moderated due to growth of animals preying upon dead shrimp.

Diets in Group I with casein as the major protein source produced little growth above sustenance. Diet 1 with an added mineral mix yielded a significantly higher biomass increase above initial weights at the 5% feeding level than either Diets 2 or 3 which lacked the mix. In addition to the mineral mix, Diet 3 lacked sodium glutamate, glycine, citric acid, and succinic acid and correspondingly caused a loss in biomass over the 3-month growth period. Although the above results showed Diet 1 to be significantly different ($P < 0.05$) from the other diets after the first month of study, results are somewhat confounded with initial differences in stocked biomasses and poor response in general.

These sustenance biomass levels represented far less growth increase than the 72% of control obtained by Kanazawa et al. (1970) and may be due to a lack of cholesterol in our study. Since many crustaceans are not able to synthesize cholesterol (Van Den Oord, 1964; Dall, 1965; Zandee, 1967), including recent evidence for shrimp (Kanazawa et al., 1971), the lack of this entity undoubtedly was attributed to the poor performance of these diets.

Shrimp fed on Group II diets averaged a 37 to 63% increase in growth. Although results from Diets 5, 6, and 7 were not significantly different ($P < 0.05$), Diet 6, which consisted of a high ratio of shrimp to fish meal and a low level of casein, yielded greatest biomass increases. Total biomass decreased in diets having a decrease in percentage of shrimp meal. Growth from Diet 8, which contained blended shrimp muscle and lower levels of shrimp and fish meal, was statistically less ($P < 0.05$) than the other three diets. Again, the control group of starved shrimp was not able to sustain its initial weight and declined in biomass after the first 2 weeks.

Group III, consisting of yeast, casein, and soy protein hydrolysate diets, produced an average biomass increase of 18 to 39% (Table 1). The combination of diets containing casein, soy, and yeast hydrolysates produced significantly better ($P < 0.05$) growth than individual hydrolysates. Since results from this group were not better than results after 6 weeks from Diet 5 which was similar except it contained only intact protein, these data indicate that hydrolyzed proteins are not utilized more efficiently than intact proteins.

Comparing food supplied at 0, 5, 10, and 15% of total biomass using Diet 6 illustrated that growth was directly proportional to an increase in feeding rate (Group IV), and may reflect the natural feeding habit of the species. While the population of starved animals disappeared after 8 weeks, the treatments fed at 5% of their biomass increased 58% over their initial weight; those fed at 10% of their biomass increased 109%; and those fed at 15% biomass gained 164%. The above results indicate that penaeids are capable of consuming large amounts of food. This may be a reflection of their natural tendency to continuously graze upon large quantities of benthic material rather than feed periodically as would a strict carnivore. Although pellets used in all experiments were textured to maintain consistency in solution for 24 hr, some shattering may occur as shrimp gnaw at them and thus some food may be lost through flushing, thus decreasing the efficiency of ingestion as feed levels are increased.

Although growth was directly proportional to an increase in feeding rate, feeding at low levels was still justified in attempting to determine nutritional requirements of shrimp. The benthic material normally grazed upon is low in energy content and is often of relatively poor nutritional content. Feeding at lower fed levels but with food of proper nutritional value could conceivably produce growth comparable to higher fed

levels of natural or formula diets presently known.

Food conversion ratios (FCR) (weight of food fed for 6 weeks/weight increase) were calculated from results in Group IV (calculated on a dry weight basis). Feeding at 10% biomass yielded an FCR of 6.7 and growth increase of 109%. On the other hand, feeding at the 15% level produced a 164% growth increase and an FCR of 5.5. Such FCR, although not comparable to those obtained for vertebrates such as the 1.6 or less for catfish (Andrews, in press), nonetheless represent a significant decrease over the FCR of 10 or greater reported for shrimp fed on natural foods (Fujinaga, 1963). Further refinement of the FCR for penaeids can undoubtedly be obtained through procurement of a more suitable pellet, better understanding of exact nutritional requirements of specific nutrients, and more information on ingestion and assimilation phenomena.

SUMMARY

1. Environmental conditions yielding 80 to 90% survival in the intensive tank culture of penaeid shrimp encompassed a combination of either no substrate or sand substrate on elevated platforms, air supplied externally by an aeration system, and population density of 40 g/m^2.

2. Diets having balanced complements of proteins, lipids, carbohydrates, amino acids, fatty acids, minerals, and vitamins produced only sustained biomass levels.

3. Diets having 69.5% of the total diet as shrimp meal produced growth increases of 63%.

4. Examination of soy, casein, and yeast hydrolysates revealed that a combination of each produced 39% growth increase while an average of 18% resulted from feeding each hydrolysate separately. Hydrolyzed proteins did not yield better growth than intact proteins.

5. Feeding at 5, 10, and 15% of the animals' biomass daily yielded directly proportional growth. A growth increase of 164% was achieved with a fish meal and shrimp meal diet fed at 15% of biomass daily.

6. Using semipurified pelleted diets, food conversion ratios were reduced by nearly half of that reported for penaeids feeding on clam and other natural foods.

7. Establishing selected preliminary environmental and nutritional requirements for penaeid shrimp resulted in reproducible production of major biomass increase with relatively high survival and low food conversion ratios.

8. Results from these studies have allowed us to design facilities and experiments for future work with environmental and nutritional factors. Development of an inexpensive diet which will yield rapid and maximum growth will be an essential requirement for economical production of penaeid shrimp.

ACKNOWLEDGMENTS

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METHOD OF DETERMINING CAROTENOID CONTENTS OF ALASKA PINK SHRIMP AND REPRESENTATIVE VALUES FOR SEVERAL SHRIMP PRODUCTS

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ABSTRACT

An extraction method is described for estimating the amount of carotenoids in pink shrimp. The carotenoid index is useful as a measure of quality and as an indicator of changes during storage. Values for several shrimp products are reported.

The carotenoid content of Alaska pink shrimp is affected by many conditions and can be used as an index of the general quality of canned shrimp and of the changes in quality of frozen shrimp during storage. It has been also used as a factor in determining optimum peeling characteristics of shrimp (Collins and Kelley, 1969) and in selecting desirable retorting conditions (Kelley, 1971[3]). Color differences in shrimp at different seasons and in different areas may be important in harvesting and marketing practices.

The carotenoid in Alaska pink shrimp is primarily astaxanthin. Both total astaxanthin and astacin, its oxidation product, are measured by the method to be described, which was developed for use with frozen Alaska king crab (Ravesi, 1965[4]) and adapted to Alaska pink shrimp which contain more interfering protein and moisture than crab.

METHOD OF DETERMINING CAROTENOID CONTENTS

To 50 g of blended meat add approximately 10 g of silica gel and 100 ml of the proper acetone solution:

1. 75% acetone for canned shrimp with liquor.
2. 65% acetone for frozen cooked or raw meats.
3. 50% acetone for raw shrimp with shells on.

The silica gel, which serves as a filter aid, is not essential but makes subsequent extraction and filtration easier. Blend just enough to ensure complete mixing and filter through a medium porosity fritted glass funnel, maintaining suction until dripping ceases. Rinse container and filter as needed with 50% acetone. Discard colorless filtrate and blend residue about 2 min with 15 to 20 g anhydrous sodium sulfate and 100 ml of 1:1 2-propanol:chloroform. Filter and re-extract with 50 ml solvent one or two times as needed to get a colorless meat. Use 2-propanol:chloroform as rinse solution during these extractions. Transfer filtrate to 500 ml round bottom flask and strip the solvent, using a rotating vacuum evaporator. Add 5 to 10 ml chloroform and evaporate to dryness. Dissolve residue in enough pure cyclohexane to wash sides of flask and add 10 to 15 g anhydrous sodium sulfate. Let set for a few minutes and filter through sodium sulfate on a fine porosity fritted

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glass funnel, washing sodium sulfate with cyclohexane to remove all traces of color. If filtrate is clear, dilute to 100 ml. If it appears hazy, repeat the filtration, allowing solution to remain in fresh sodium sulfate for a brief time. Read at 474 nm on spectrophotometer, using cyclohexane as a blank.

The precision of the method was determined by analyzing 11 identical samples in quadruplicate on 11 different days. Twenty-two cans of the same code of canned shrimp were blended in a Waring blendor, and the homogeneous mixture was sealed in cans and frozen at —60° F. For each day's sampling, two cans of the frozen mixture were thawed and blended together.

Different lots of solvents were used at intervals to determine the sensitivity to slight variations in solvents. The solvent lot was not critical but the cyclohexane used in the spectrophotometer should be carefully distilled within a few days of use. We used a Gilford modification of a Beckman DU spectrophotometer[5] which gives readings with three place accuracy. The range of absorbance readings was 0.420 to 0.452, the average was 0.436, and the standard deviation was 0.008.

The carotenoid content, expressed as the carotenoid index, is a calculated value based on dry weight. The solids content of the shrimp was determined by the Association of Official Agricultural Chemists method (Horwitz, 1965: 346), using 5 to 10 g of the blended meat sample and heating at 105° C for 18 to 24 hr. The carotenoid index represents the absorbance (A) in 100 ml of solvent of the carotenoids from 1 g of dry sample, measured in a 1-cm cell. It is calculated as follows:

$$C_I = \frac{(\text{A at 474 nm in 100 ml cyclohexane})\,(100)}{(\text{50-g wet sample})\,(\%\ \text{dry weight})}$$

The absorbance reading of a shrimp sample with average moisture content is roughly 10 times larger than the carotenoid index; therefore the carotenoid index equivalent of the standard deviation is slightly less than 0.001.

[5] The use of trade names is merely to facilitate description and does not imply endorsement of a product.

The amount of carotenoid can also be expressed as grams of pigment/gram tissue by using the extinction coefficient of 2150, as reported by Kanemitsu and Aoe (1958). The amount of astacin present in fresh shrimp is small and since the extinction coefficients of astacin and astaxanthin for calculation purposes do not introduce significant error for routine analytical work, the calculation would be:

$$\text{grams pigment/1 g tissue} = \frac{(A \text{ at } 474 \text{ nm})\,(100 \text{ ml})}{100\ (50\text{ g})\ (d)\ (2150)}$$

where d is the cell width in centimeters. This could be converted to dry tissue weight by multiplying by the percent of solids in the sample.

CAROTENOID CONTENTS OF VARIOUS TYPES OF SHRIMP SAMPLES

Table 1 gives carotenoid values of various types of shrimp samples described. Most of the data were collected as part of some other project so these samples are from several lots of shrimp caught at different times of the year. Only those grouped together in the table can be accurately compared with each other. All data, however, represent an average figure for the given sample and may be used to compare types of sample products or processing methods.

TABLE 1.—Carotenoid values for 11 shrimp samples.

	Sampling conditions	Carotenoid index	Cause of color differences indicated by data
1.	Raw tails, shells on	0.237	
	Raw meats	0.086	
2.	Whole cooked, hand-peeled meats, frozen	0.112	
3.	Precooked, machine-peeled meats, frozen	0.086	
	After 6 months' storage	0.070	Storage time
	After 12 months' storage	0.062	
4.	Precooked, machine-peeled canned	0.073	Precook versus ice held conditioning
	2-day iced, machine-peeled, canned	0.059	
5.	1-day not iced, precooked, machine-peeled, canned	0.080	
	2-day iced, precooked, machine-peeled, canned	0.066	Time of ice holding
	3-day iced, precooked, machine-peeled, canned	0.064	

EXPERIMENTAL PROCEDURE

1. The shrimp were frozen whole as soon as possible after being caught, then were shipped to the laboratory. They were partially thawed, weighed, and separated according to weights. The shrimp used were about 80 count. All were headed and some were hand peeled to obtain meats. The tails with shells on and the peeled meats were refrozen as needed until analyses could be made.

2. Whole cooked, hand-peeled frozen shrimp meats were obtained from a commercial processor. This is the conventional, cocktail style product.

3. Precooked, machine-peeled shrimp were produced under experimental conditions in a commercial plant. Shrimp were landed within 24 hr of catching, held overnight without ice, and precooked at 165° F for 10 sec, 110° F for 2 min, and machine peeled. The meats were collected at the end of the inspection belt and frozen in cans without vacuum. Analyses were made within a few days, after 6 months, and after 12 months of 0° F storage.

4. Precooked, machine-peeled canned shrimp were produced as described above except they were routinely retorted. The 2-day iced, machine-peeled shrimp are a standard commercial pack from the same lot of shrimp.

5. The 1-day not iced; 2-day iced; and 3-day iced, precooked machine-peeled, canned shrimp were also experimentally produced in a commercial plant. The 1-day not iced shrimp were held in the wooden boxes in which they were landed. The 2- and 3-day iced shrimp were held in large tanks and ice added as needed to keep them cool. All of these shrimp were precooked at 165° F for 10 sec, 110° F for 2 min, and then routinely peeled and canned.

All samples were analyzed using the previously described method of determining carotenoid contents. The averages reported in Table 1 represent 3 to 12 determinations under the given sampling conditions.

Some of the factors which cause differences in the carotenoid content of shrimp are shown in Table 1. These include several processing variations which can be controlled by processors and fishermen.

CONCLUSIONS

The method of determining carotenoid content described is simple and precise and may be used on a variety of shrimp product forms.

The carotenoid index for Alaska pink shrimp varies from 0.267 in raw tails to 0.059 in ice held, machine-peeled canned shrimp. Correlation with subjective color rating is quite good (Collins and Kelley, 1969). At the higher color levels found in raw, hand-picked, or precooked shrimp, small differences are difficult to detect visually and the determination of the carotenoid index becomes even more useful in evaluating samples.

Since the carotenoid content is usually closely correlated with other quality characteristics, the carotenoid determination may be useful in making decisions about the best ways to process or handle shrimp.

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A DESCRIPTION OF YOUNG ATLANTIC MENHADEN, *Brevoortia tyrannus*, IN THE WHITE OAK RIVER ESTUARY, NORTH CAROLINA

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ABSTRACT

Atlantic menhaden exhibit three different stages—larva, prejuvenile, and juvenile—during their stay in the estuary. For specimens collected from the White Oak River estuary, N.C., the length-weight relation was $\log_e \hat{Y} = -8.1104 + 3.6050 (\log_e X)$ for larvae, $\log_e \hat{Y} = -16.9638 + 6.3083 (\log_e X)$ for prejuveniles, and $\log_e \hat{Y} = -5.2298 + 3.1452 (\log_e X)$ for juveniles, where $Y =$ weight in mg and $X =$ length in mm. Larvae and prejuveniles concentrated in the low salinity-freshwater zone upstream. Juveniles tended to move downstream toward the higher salinity water. Condition factors of larvae and prejuveniles increased toward the higher salinity zone.

Atlantic menhaden spawn and hatch in coastal oceanic waters from Maine to Florida. The larvae enter estuaries where they transform into juveniles near the freshwater zone. The relation of young menhaden length and weight to time, salinity, and location within an estuary provides insight on the environmental requirements of menhaden during a critical phase in their life cycle. We collected young menhaden from a small estuary in North Carolina, from March to September 1969 with a tidal net (Lewis et al., 1970) to study changes in the length-weight relation.

The lower portion of the White Oak River estuary (28 sq km) is shallow with depths from 0 to 3.0 m and distances from opposing shores from 1 to 3 km. The intracoastal waterway crosses the lower estuary and is maintained at a depth of approximately 4 m. The upstream portion narrows into a river up to 4.6 m deep. During the study period we generally found that the change from brackish to fresh water occurred between 18 and 24 km upstream from Bogue Inlet. The exact location of this low salinity zone was influenced by tide, rainfall, and direction and speed of the wind. The mean tidal range at Bogue Inlet is 2.2 ft (0.67 m) (U.S. Coast and Geodetic Survey, 1970). At 21 km upstream the average river flow is 14.7 cfs (0.42 m^3/sec) (North Carolina State Board of Health, 1954). A map showing the location of the White Oak River estuary is shown in Lewis and Mann (1971).

We selected 14 stations from Bogue Inlet to 34 km upstream (Wilkens and Lewis, 1971). Stations ranged from 2 to 5 km apart and were selected to be representative of the various salinities encountered. We also sampled in fresh water to determine how far menhaden move upstream. Salinity measurements were taken within 1 m of the surface. During collections, spot checks of salinity between the surface and bottom indicated that in this shallow estuary thorough mixing generally occurred. Differences between measurements at one location were due to flooding and ebbing tides.

Our menhaden collections ranged from 15 to several thousand individuals. We measured and weighed all fish to the nearest 0.5 mm total length and 0.1 mg in collections containing less than 26 and subsampled the larger collections. Since both length and weight variances in the subsamples were small, we considered our estimates of length and weight to be reliable. Our measurements of total length were based on the greatest dimension between the most anteriorly projecting part of the head and the farthest tip

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of the caudal fin when the caudal rays are squeezed together (Hubbs and Lagler, 1949).

We separated young menhaden into three stages on the basis of body form and the length-weight relation of individuals within each stage. Length and weight ranges of all the fish used in the study are given in Table 1. An illustration of each stage (larva, prejuvenile, and juvenile) that occurs during the first year in the estuary is shown in Figure 1.

Allometric growth, with stanzas for larvae, prejuveniles, and juveniles is shown in Figure 2. The inflection points, indicating change in slope, are 30 and 38 mm for length, and 70 and 469 mg for weight. We considered specimens less than 30 mm and 70 mg as larvae; they are long and slender, and even at 30 mm total length the body depth is only 4 mm or less. In the next group,

TABLE 1.—Lengths and weights of Atlantic menhaden from the White Oak River estuary, N.C., arranged in order of increasing weight classes.

Weight	Length range	Number of menhaden	Weight	Length range	Number of menhaden
mg	mm		mg	mm	
0.0- 4.9	8-16	23	100.0- 199.9	29-34	38
5.0- 9.9	14-20	46	200.0- 299.9	33-37	26
10.0-14.9	17-21	43	300.0- 399.9	35-38	6
15.0-19.9	20-23	48	400.0- 499.9	37-43	5
20.0-24.9	20-24	45	500.0- 599.9	39-41	10
25.0-29.9	22-26	32	600.0- 699.9	40-44	14
30.0-34.9	23-26	30	700.0- 799.9	41-44	11
35.0-39.9	24-27	31	800.0- 899.9	44-45	6
40.0-44.9	25-28	29	900.0- 999.9	45-49	4
45.0-49.9	25-29	10	1,000.0-1,499.9	47-54	41
50.0-54.9	26-29	20	1,500.0-1,999.9	53-60	27
55.0-59.9	27-29	26	2,000.0-2,499.9	58-62	16
60.0-64.9	27-31	26	2,500.0-2,999.9	61-66	11
65.0-69.9	27-31	19	3,000.0-3,499.9	68-71	5
70.0-74.9	28-31	22	3,500.0-3,999.9	71-74	8
75.0-79.9	29-32	15	4,000.0-4,499.9	75-77	4
80.0-84.9	29-32	12	4,500.0-4,999.9	76-82	5
85.0-89.9	29-31	7	5,000.0-5,499.9	81	3
90.0-94.9	28-32	11	5,500.0-5,999.9	81-83	2
95.0-99.9	29-32	6			

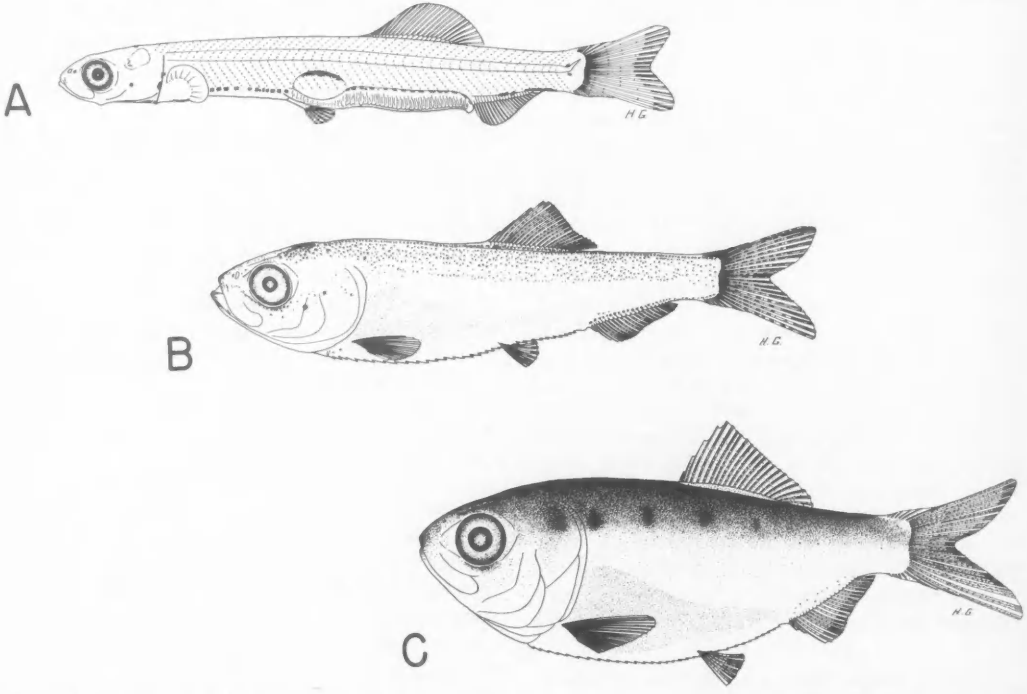

FIGURE 1.—Atlantic menhaden (a) larva 27.0 mm total length (TL); (b) prejuvenile 32.0 mm TL; and (c) juvenile, 64.0 mm TL. The alimentary tracts are shown as they were visible in the preserved specimens used in drawings.

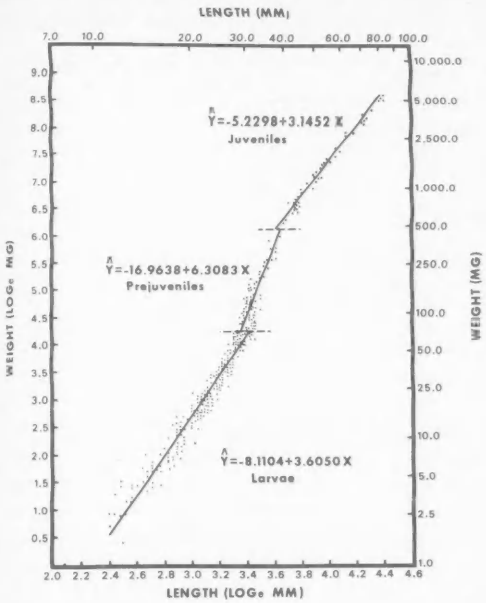

FIGURE 2.—Regression of weight on length for larval, prejuvenile, and juvenile Atlantic menhaden collected in White Oak River estuary, N.C., in 1969. (We separated the lengths and weights into three groups after visual observation of the data and fish. Lines were then fitted by least squares regression based on data in each group.)

prejuveniles, we included specimens from 30 to 38 mm and 70 to 469 mg. In this stage there is a rapid increase in body depth, but little increase in length. Fish above 38 mm and 469 mg we classed as juveniles. Huntsman[3] found that the relation between length and weight is similar for juveniles and adults. Both stages have a similar body form, only their color and size being different. We did not find any adults in our estuarine study.

Larvae enter the lower estuary and move upstream to the freshwater-low salinity zone where they go through a prejuvenile stage before completing their transformation into juveniles.

[3] Huntsman, Gene R. 1971. Growth by year class of Atlantic menhaden. (Unpublished manuscript.) NMFS Center for Estuarine and Menhaden Research, Beaufort, NC 28516.

Larval menhaden were most abundant in March, prejuveniles in late March and April, and juveniles by the beginning of May (Wilkens and Lewis, 1971). Large catches of larval and prejuvenile menhaden within the freshwater-low salinity zone (Table 2) suggest that favorable conditions for growth are present.

Condition factors (W/L^b, where W = weight in mg, L = length in mm, and b = value for the slope of weight on length for each growth stanza) of larvae and prejuveniles increased with time as the result of growth and development. The apparent lack of growth of larvae and prejuveniles in the low salinity-freshwater zone during April is probably due to large numbers entering this zone, putting on fast growth, moving out of the zone, and being replaced by new groups (Tables 2 and 3). Juveniles, which have the same body form as adults and which are scattered in schools throughout the estuary, showed no change in condition factor with time or salinity.

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TABLE 2.—The distribution and mean total length (mm) of menhaden by date collected, kilometers upstream from Bogue Inlet, and salinity (‰) in the White Oak River estuary, March-August 1969.

	Date 1969										
	Mar. 17	Mar. 27	Apr. 1	Apr. 9	Apr. 16	May 1	May 14	May 27	June 26	July 16	Aug. 27
16 kilometers:											
Salinity	--	0	1.5	4.1	8.0	5.2	13.7	15.4	1.8	10.2	15.1
Abundance index[1]	--	4.3	298.4	48.8	111.0	279.1	0.1	5.2	4.2	4.6	0.3
Mean total length	--	28.5	28.9	30.0	29.2	32.1	--	42.4	53.4	58.8	--
18 kilometers:											
Salinity	1.5	0	0.2	0.1	3.8	1.8	7.4	11.7	0.2	3.0	8.9
Abundance index	9.6	0.4	1,053.4	497.7	526.5	155.2	0.4	1.1	16.3	6.6	0
Mean total length	29.9	--	28.5	27.5	30.8	30.5	--	--	43.5	51.0	--
21 kilometers:											
Salinity	0.2	0	0	0	1.2	--	4.2	--	--	--	--
Abundance index	48.7	0	54.2	65.3	0	--	0.5	--	--	--	--
Mean total length	30.8	0	28.3	27.2	--	--	--	--	--	--	--
24 kilometers:											
Salinity	0	0	0	0	0	0	1.5	4.4	0	0	0.5
Abundance index	13.3	1.8	6.0	1.5	1,533.3	392.6	0.7	13.9	0.4	1.4	1.0
Mean total length	30.1	29.6	29.2	26.6	28.5	29.4	--	42.6	--	--	--
28 kilometers:											
Salinity	0	0	0	0	0	0	0	0.6	0	0	0
Abundance index	0	0.5	1.4	0.2	0.6	0	0.1	12.1	0.3	0.2	0
Mean total length	--	--	29.5	--	--	--	--	41.8	--	--	--
31 kilometers:											
Salinity	0	--	0	0	0	0	0	0	0	--	--
Abundance index	0	--	0.3	10.3	0	0	0	1.0	0	--	--
Mean total length	--	--	--	29.1	--	--	--	--	--	--	--

[1] Abundance index is the number of young menhaden for 100^3 of water.

TABLE 3.— Mean condition factors of young Atlantic menhaden collected in the White Oak River estuary, N.C., in 1969.

	Date	Salinity (‰)							
		0	0.1-0.9	1.0-1.9	2.0-2.9	3.0-3.9	4.0-4.9	5.0-5.9	>6.0
	1969								
Larvae	Mar. 17	0.292	0.303	0.253	--	--	--	--	--
	Mar. 27	0.293	--	--	--	--	--	--	--
		0.302	--	--	--	--	--	--	--
	Apr. 1	0.291	0.309	0.331	--	--	--	--	--
		0.332	--	--	--	--	--	--	--
		0.310	--	--	--	--	--	--	--
	Apr. 9	0.331	0.326	--	--	--	0.326	--	--
		0.317	--	--	--	--	--	--	--
		0.355	--	--	--	--	--	--	--
	Apr. 16	0.321	--	--	--	0.357	--	--	0.444
	May 1	0.358	--	--	--	--	--	--	--
Prejuveniles	Mar. 17	0.299	0.305	0.314	--	--	--	--	--
	Mar. 27	0.394	--	--	--	--	--	--	--
		0.376	--	--	--	--	--	--	--
	Apr. 1	0.342	0.387	0.390	--	--	--	--	--
		0.364	--	--	--	--	--	--	--
		0.381	--	--	--	--	--	--	--
	Apr. 9	0.396	0.435	--	--	--	0.420	--	--
	Apr. 16	0.402	--	--	--	0.476	--	--	0.516
	May 1	0.497	--	0.599	--	--	--	0.547	--
	May 27	--	0.555	--	--	--	--	--	0.498
Juveniles	May 27	--	0.551	--	--	--	0.517	--	0.507
	June 26	--	0.526	0.540	--	--	--	--	--
	July 16[1]	--	--	--	--	0.542	--	--	0.535

[1] Sample sizes after July 16 were too small to show trends.

GROWTH OF PREMIGRATORY CHINOOK SALMON IN SEAWATER

BERNARD M. KEPSHIRE, JR., AND WILLIAM J. MCNEIL[1]

ABSTRACT

A potential demand exists in sea farming for premigratory juvenile Pacific salmon that have been acclimated to seawater. This paper reports experiments on growth of premigratory chinook salmon (*Oncorhynchus tshawytscha*) acclimated to water of 33‰ salinity and lower and describes a simple mathematical model to evaluate rate of growth. Although chinook salmon raised in these experiments experienced low mortality in water of high salinity, their growth slowed. Reasons for slow growth at high salinity are discussed.

Pacific salmon reproduce in fresh water, but only two species—pink (*Onchorhynchus gorbuscha*) and chum (*O. keta*) salmon—survive direct transfer as fry from fresh water to full-strength seawater (Weisbart, 1968). The ocean serves as the early nursery ground for these two species. The other species—including sockeye (*O. nerka*), coho (*O. kisutch*), and chinook (*O. tshawytscha*) salmon—require freshwater nursery areas.

Juvenile salmon undergo a period of adjustment when they first enter the sea in order to regulate water and salts in body fluids and tissues. This adjustive phase for chum salmon fry lasts about 30 hr and is characterized by an immediate depression of activity, increased concentration of salts in body fluids, and dehydration of body tissues (Houston, 1959). A slightly longer adjustive phase of 36 to 40 hr has been reported for yearling coho salmon (Conte et al., 1966; Miles and Smith, 1968).

Early exposure to water of low salinity can "trigger" the physiological adaptation to seawater of salmon species which typically remain in fresh water for several months as juveniles. Acclimation of premigratory young chinook salmon to water of 30‰ salinity by exposing them to gradual increments in salinity has been described by Wagner et al. (1969). Black (1951), Coche (1967), and Otto (1971) found also that coho salmon fry were better able to tolerate water of high salinity after having first been exposed to water of low salinity.

Other evidence suggests that the growth of juvenile coho and chinook salmon is influenced by salinity. Coho salmon fry were observed by Canagaratnam (1959) to grow faster in water of 12 to 18‰ than in fresh water. Otto (1971) reported faster growth of juvenile coho salmon at 5 and 10‰ salinity than at higher salinities or in fresh water. Bullivant (1961) found no significant difference in growth of juvenile chinook salmon in water of 0 and 18‰ salinity. However, Bullivant's fish grew more slowly at 35‰ salinity than at the two lower salinities.

This paper reports comparisons of the growth of juvenile chinook salmon raised in water ranging in salinity from 0 to 33‰. The experiments were conducted at the Oregon State University Port Orford Marine Research Laboratory, Curry County, Oreg.

GENERAL PROCEDURES

Two groups of chinook salmon used in these experiments were obtained as eyed eggs from the Fish Commission of Oregon, Elk River Hatchery, in winter 1969. Group I fish were divided into five subgroups of 200 each on February 24 (47 days after hatching). Group II fish were divided into six subgroups of 300 each on March 5 (18 days after hatching). Individual subgroups were introduced to water of

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increasing salinity according to the schedules outlined in Tables 1 and 2.

Both groups of fish received the Oregon Moist Pellet diet. The young salmon were fed five times daily beginning 30 days after hatching. After the fish had attained an average weight of 1 g, the frequency of feeding was reduced to three times daily. They were provided more food than they would consume at each feeding.

Fish were raised in 100-gal plywood tanks which were lined with fiber glass. Water was introduced to each tank at the rate of one-half gallon per min. Incoming fresh and salt water were premixed in head tanks to obtain desired salinities. Salinities were calculated from the proportions of premixed seawater and fresh water, and density of water in fish tanks was measured periodically with hydrometers to insure that salinities remained at their calculated levels.

The first experiment (Group I fish) began on January 8 with newly hatched alevins. Group I fish first received food on February 7, and selected subgroups were exposed to water of 9 or 17‰ salinity beginning on February 24. The five subgroups were first weighed on February 27. The experiment ended on May 7.

The second experiment (Group II fish) began on February 16 with newly hatched alevins. All six subgroups of fish were first exposed to water of 5 or 9‰ salinity on March 6 while still in the alevin stage, and they remained at these salinities for 18 days. The fish were first fed on March 18 and first weighed on April 7. The experiment ended on May 6.

Mortality of the 11 subgroups of fish during the test periods ranged from 0 to 6% of the original number of fish placed in the tanks. Even the maximum mortality (6%) was considered to have no appreciable effect on the comparisons of growth.

The average wet weight of fish in each subgroup was determined at 14-day intervals from random samples of 30 fish. Excess water was blotted from anesthetized fish before weighing. Fish were weighed separately in a flask containing a known weight of water and were returned to their respective tanks after each weighing.

TABLE 1.—Exposure of Group I chinook salmon to water of increasing salinity. Date of hatch—January 7, 1969.

Subgroup	Age (days after hatching) at which fish were placed in water[1] of given salinity		
	47	66	80
	‰	‰	‰
Ia	0	0	0
Ib	9	17	17
Ic	17	17	33
Id	17	24	33
Ie	9	24	33

[1] Temperature of incoming water averaged 10.7° C for fresh water and 10.8° C for seawater.

TABLE 2.—Exposure of Group II chinook salmon to water of increasing salinity. Date of hatch—February 15, 1969.

Subgroup	Age (days after hatching) at which fish were placed in water[1] of given salinity			
	18	36	54	66
	‰	‰	‰	‰
IIa	5	18	18	18
IIb	9	18	18	18
IIc	5	18	25	33
IId	5	18	25	33
IIe	9	18	25	33
IIf	9	18	25	33

[1] Temperature of incoming water averaged 11.9° C for fresh water and 12.0° C for seawater.

OBSERVATIONS ON GROWTH

Growth rate was calculated for each subgroup from the periodic measurements of wet weight. Growth was assumed to be exponential over each period considered, and a value for the daily increment in body weight, which can be expressed as a percent of body weight per day, was obtained from the expression

$$\frac{W_t}{W_0} = (1 + h)^t \qquad (1)$$

where W_t = weight at the end of the period,
W_0 = weight at the beginning of the period,
h = the compounded daily increment of body weight, and
t = days.

It is convenient to solve equation (1) for $(1 + h)$ by converting the terms to common logarithms and taking the antilog, i.e.

$$\log (1 + h) = \frac{\log W_t - \log W_0}{t} . \qquad (2)$$

To clarify the concept of daily increment of body weight, fish that can maintain an increase in body weight of 2.0 and 3.0% per day, for example, will double their weight in approximately 35 and 23 days, respectively.

Fish held in water of 0, 17, and 18‰ salinity grew at a faster rate and were heavier at the end of the experiments than fish of the same age transferred to water of 24, 25, and 33‰ salinity. The observed mean weight of fish in individual subgroups is plotted against age of fish in Figure 1.

Equation (2) can be rewritten in linear form to calculate statistics which are useful for making comparisons of rate of growth among test groups of fish. The linear model is:

$$(\log W_t - \log W_0) = \log (1 + h) \cdot t \quad (3)$$

Slope of the regression line is given as log $(1 + h)$. This model requires the regression line to pass through the origin since $(\log W_t - \log W_0) = 0$ at $t = 0$.

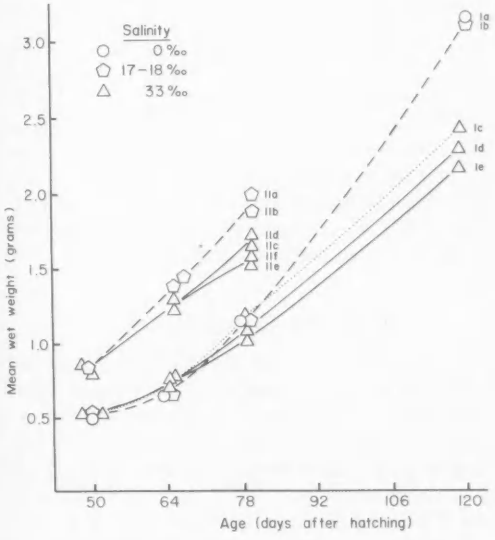

FIGURE 1.—Growth in weight of experimental subgroups of juvenile chinook salmon.

Group I fish were weighed on six occasions over a period of 70 days. We have estimated values of log $(1 + h)$ and h for each of the five subgroups of Group I by calculating the five regressions of $(\log W_t - \log W_0)$ on t. Because the weight of Group II fish was measured on only three occasions, we have not applied a similar analysis to the second experiment.

Application of regression methods to observations on Group I fish indicates that fish in fresh water and water of 17‰ salinity (Subgroups Ia and Ib) grew at a significantly faster rate than fish exposed to water of 33‰ salinity (subgroups Ic, Id, and Ie). Equations for the five subgroups are given in Table 3 along with the 95% confidence interval estimates of log $(1 + h)$ and the approximate confidence interval estimates of h. Figure 2 shows growth curves for the fastest (Subgroup Ia) and slowest (Subgroup Ie) growing fish. The periodic measurements of weight are plotted in Figure 2 to show their correspondence with the growth curves calculated by use of equation (1).

DISCUSSION

Chinook salmon used in these experiments were exposed to salt water much earlier in life than they normally would experience in nature. Group I fish were acclimated to high salinity (24‰) 66 days after hatching and 36 days after commencement of feeding. Group II fish were acclimated to high salinity (25‰) 54 days after hatching and 24 days after commencement of feeding. There were only 66 deaths (3.7%) among the 1,800 fish which had been exposed to salinities of 24, 25, and 33‰ for periods of 25 and 54 days.

The average rate of growth in water of high salinity (24‰ and above) varied between 2.1 and 2.3% increment in body weight per day. These fish doubled their weight in 30 to 33 days. The average rate of growth in water of low salinity (17‰ and 0‰) was 2.6 and 2.7% per day. These fish doubled their weight in 26 to 27 days.

Although these experiments demonstrate that juvenile chinook salmon can be acclimated to full-strength seawater in an early age, it is apparent that water of high salinity causes a reduced rate

TABLE 3.—Regression of (log W_t − log W_0) on time for Group I fish. The approximate 95% confidence interval estimates of h are taken from the confidence limits of log $(1 + h)$.

Subgroup	Regression equation	95% confidence limits of log $(1 + h)$	Approximate 95% confidence limits of h
Ia	(log W_t − log W_0) = 0.01168t	0.01168 ± 0.00099	2.7 ± 0.2%/day
Ib	(log W_t − log W_0) = 0.01118t	0.01118 ± 0.00084	2.6 ± 0.2%/day
Ic	(log W_t − log W_0) = 0.01006t	0.01006 ± 0.00087	2.3 ± 0.2%/day
Id	(log W_t − log W_0) = 0.00945t	0.00945 ± 0.00077	2.2 ± 0.2%/day
Ie	(log W_t − log W_0) = 0.00880t	0.00880 ± 0.00042	2.1 ± 0.1%/day

of growth. Reduced growth may come about in part because the young salmon expend more energy to maintain an osmotic homeostasis in water of high salinity than in water of low salinity.

Chinook salmon blood is isotonic with water of salinity between 10 and 13‰ (Coche, 1967). Houston (1959) thought that the increased energy demands for osmoregulation combined with possible inhibition of electrolyte-sensitive components of the neuromuscular system might contribute to reduced growth of young salmon in water of high salinity. There is the further possibility that endocrine systems which are associated with osmoregulation and growth in water of high salinity are not fully functional in premigratory juvenile salmon (Saunders and Henderson, 1970).

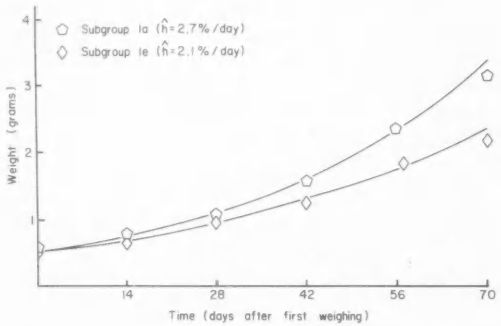

FIGURE 2.—Calculated growth curves for chinook salmon from subgroups Ia and Ie as calculated from equation (1). The observed growth is plotted to illustrate correspondence with calculated curves. "h" is the compounded daily increment of body weight.

The acclimation of premigratory chinook, coho, and sockeye salmon to seawater may find future applications in aquaculture. Possibilities include the early release of young salmon from hatcheries into open ocean pastures to reduce costs of feeding and handling and to increase hatchery production. Other possibilities are to pen young salmon in saltwater bays or estuaries (Garrison, 1965; Mahnken et al., 1970) or to place them in raceways receiving waste salt water from coastal thermal-electric stations (McNeil, 1970).

Large-scale aquaculture systems, similar to one under development in the Canadian Maritime Provinces (Gunstrom, 1970), would most likely benefit from early acclimation of juvenile salmon to seawater. The release of premigratory juvenile chinook salmon acclimated to seawater should also be tested at hatcheries equipped with seawater pumping systems. The effects of early acclimation on ocean survival is unknown, but the greater availability of food and space in the ocean than in freshwater conceivably would provide potential advantages to juvenile salmon which had been acclimated to seawater.

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EFFECT OF ENCROACHMENT OF WANAPUM DAM RESERVOIR ON FISH PASSAGE OVER ROCK ISLAND DAM, COLUMBIA RIVER

RICHARD L. MAJOR[1] AND GERALD J. PAULIK[2]

ABSTRACT

The filling of Wanapum Reservoir in 1964 flooded the lower sections of the three fish ladders at Rock Island Dam, 61 km upstream from Wanapum Dam on the Columbia River. To maintain fish passage under the new hydraulic conditions, the lower portions of the center and left-bank fish ladders of Rock Island Dam were rebuilt and a new sequence of spill patterns inaugurated. The effectiveness of these modifications was evaluated by comparing results from a series of tagging experiments conducted in 1964-65 on spring chinook salmon (*Oncorhynchus tshawytscha*) and sockeye salmon (*O. nerka*) with the results of similar experiments in 1954-55 before Wanapum Dam was built. These comparisons indicated fish passage over Rock Island Dam had improved substantially between 1954-55 and 1964-65; tagged fish traveled over the dam in a shorter time, and higher percentages of the tagged groups were sighted passing over the dam under postencroachment conditions.

Successful reproduction of Pacific salmon (*Oncorhynchus* spp.) and steelhead trout (*Salmo gairdneri*) requires that sufficient numbers of adults in suitable physical condition reach the spawning grounds. Serious consequences can result from delays en route. Thompson (1945), for example, showed that very few of the sockeye salmon (*O. nerka*) that were delayed more than 12 days by the Hell's Gate rock slide (Fraser River, British Columbia) reached their spawning grounds. Thompson also suggested that shorter delays reduced the reproductive capability of the survivors. Similarly, man-made facilities such as hydroelectric dams, even though equipped with fish-passage facilities, can act as barriers and thus delay or otherwise interfere with the migratory behavior of salmonids on their way to the spawning grounds.

One of the primary goals of the agencies responsible for conserving the fish resources of the Columbia River is to seek ways of minimizing the effects of dams on the migration and spawning success of the river's populations of salmonids. Although a variety of solutions to the problem of dams impeding the passage of migrating spawners have been proposed and a number of these have been tried in the field, the pool type of ladder has proven to be the only practical means of passing large numbers of adult salmonids over the dams on the Columbia River. Many research studies aimed at improving fish passage have been conducted over the past several decades. One result of this research has been the introduction of a number of improvements in design and operation of the pool-and-weir ladder. In some cases fish passage over ladders can be substantially improved by modification of spill patterns (Leman and Paulik, 1966).

The present study was designed to evaluate the effectiveness of modifications in the fish ladders at Rock Island Dam and changes in the spill pattern which were made after the lower portions of the ladders were flooded by the reservoir of Wanapum Dam. This type of problem is apt to become more common as all existing sites for hydroelectric dams are utilized and the reservoir of one dam begins to encroach on the tailrace of the dam immediately above.

Rock Island Dam, completed in 1934, was the first dam built on the Columbia River. It is in central Washington and about 725 km above the river's mouth (Figure 1). Originally, the dam

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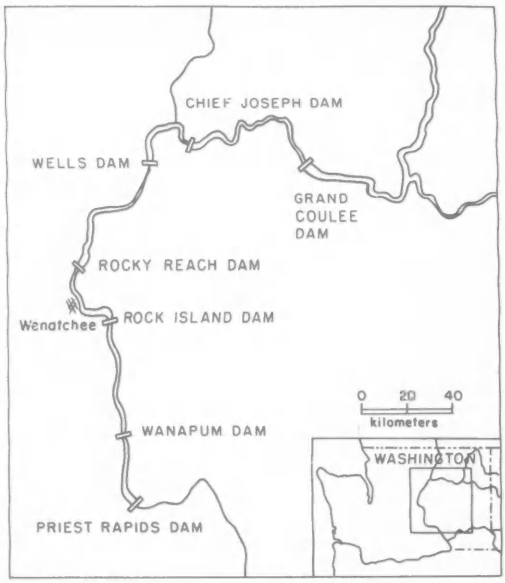

FIGURE 1.—The Columbia River and locations important to the present study.

was provided with two pool- and weir-type fish ladders, one adjacent to each bank. A third was added near the middle of the dam in 1936.

Rock Island Dam was modified during 1951-53. Six new generating units were added to the powerhouse (on the left side of the dam looking downstream), the reservoir was raised about 3.7 m, and regulating lift gates were installed in spillway bays 16-37 on the right side of the dam (Figure 2). Turbine discharge was increased from about 793 to 2,265 m^3 per sec, the fish ladders were altered to enable them to function at the new reservoir level, and the attraction flow at the entrance to the left ladder was increased to counteract the increased discharge from the turbines. Although the fishery agencies requested changes at the lower end of the right ladder to provide better entrance conditions and additional attraction flow, no immediate action was taken to implement these requests.

The Federal Power Commission, in granting permission for the modification of the dam, reserved the right to require alteration of the lower end of the right-bank ladder if substantial evidence were presented to show that alteration was necessary to protect runs of anadromous fish. Any such alteration was to begin before December 1, 1960.

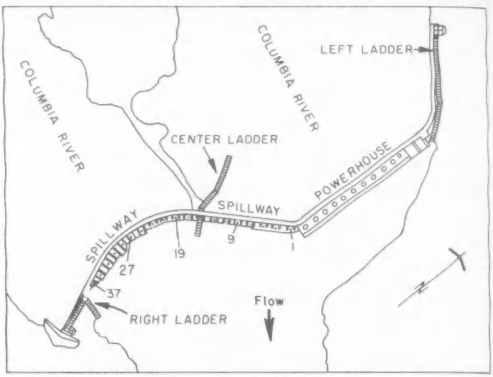

FIGURE 2.—Rock Island Dam showing locations of the fish ladders, powerhouse, and spillway bays.

To determine whether the dam caused loss or delay to the runs and whether loss or delay was associated with the right-bank fishway, tagging studies were conducted in 1954-56. French and Wahle (1966) summarized the results as follows:

> Point estimates of sockeye salmon losses ranged from 0 to 42 percent. Tagging results (one season only) on spring chinook salmon indicated a loss of fish released below the right bank ladder, but no loss when total tag returns from below and above dam releases were compared; data failed to show the dam caused losses of summer chinook. Tagged salmon released below the dam were delayed 2 to 4 days. Altering the right bank fishway may cause more fish to use it, but there is no clear evidence that such alteration will reduce overall loss or delay.[3]

Although the evidence did not indicate that a major overhaul of the right-bank ladder was justified, one relatively minor change was made. In 1956, a concrete wall was built at the entrance to the ladder. This wall replaced a cyclone fence

[3] Seasonal races of chinook salmon (*O. tshawytcha*) in the Columbia River system are classified as spring, summer, or fall chinook depending on the time of year that the adults enter the river to spawn.

which, at high tailwater elevations, appeared to impede the entry of fish into the ladder. The wall also eliminated the surging action across the ladder that occurred under certain combinations of spill pattern and tailwater elevation.

Even after these changes, fishery biologists continued to voice concern over the effectiveness of the right-bank ladder. Some held that hydraulic conditions at the entrance to the right-bank ladder impeded fish passage over the ladder. In 1958, in response to the continuing concern about the fish-passage conditions at Rock Island Dam, the owners of the dam—Puget Sound Power and Light Co. and Public Utility District No. 1 of Chelan County—financed a study to determine if fish passage could be improved by manipulating the spill pattern.

The study showed that fish could be guided to either the right or center ladders by spilling adjacent to the respective ladder. The experiment also indicated, but not conclusively, that when low tailwater elevations prevailed, spilling from gates 35, 36, and 37 (immediately adjacent to the right-bank ladder) confused the fish and interfered with their entry into the ladder (Leman and Paulik, 1966).

The construction in 1960-64 of Wanapum Dam, 61 km downstream, brought about a further change in fish-passage conditions at Rock Island Dam. The lower portions of the fish ladders at Rock Island Dam were flooded by Wanapum Reservoir. This condition, in the judgment of the Federal Power Commission, required certain modifications of the left and center fish ladders. The modifications were completed by 1963—1 year before Wanapum Reservoir was filled. The Commission also directed the owners of Rock Island Dam and of Wanapum Dam (Public Utility District of Grant County) to develop, in cooperation with representatives of the U.S. Department of the Interior and the Washington State Departments of Fisheries and Game, a program for the study and evaluation of the further effects of encroachment by Wanapum Reservoir on fish passage at Rock Island Dam.

It is important to note that the question at hand was the effect of the encroachment of Wanapum Reservoir on fish passage at Rock Island Dam and not the effects of Wanapum Dam on fish passage in the broader sense, i.e., passage over Wanapum Dam itself and passage through the newly formed forebay.

Representatives of the participating agencies formed the "Rock Island Study Group" and engaged the junior author as a consultant to serve as chairman of the group. A major segment of the research program, initiated and supervised by the study group, consisted of a series of tagging experiments conducted under postencroachment conditions. These experiments were so designed that the results would be comparable to results available from preencroachment tagging in 1954-55 (French and Wahle, 1966).[4] The field work was conducted by experienced personnel of the National Marine Fisheries Service (formerly the Bureau of Commercial Fisheries) under the supervision of the senior author.

In this paper we describe tagging experiments at Rock Island Dam in 1964-65 and compare the results to those obtained in the earlier (1954-55) study. The primary purpose is to estimate the differences between the times required for sockeye and spring chinook salmon (*O. tshawytscha*) to move from tagging sites below Rock Island Dam to the counting stations in the three (left, center, and right) fish ladders before encroachment and after encroachment.

EXPERIMENT RATIONALE

The basic experimental measures obtained from this type of tagging are (1) elapsed time from the release of tagged fish below Rock Island Dam to the sighting of tagged fish as they passed through a counting station near the top exit of the fish ladders and (2) the percentage of each release group passing over the dam. The elapsed times include (a) the time, if any, required for tagged fish to recover from possible effects of tagging, (b) the time required to locate and enter the fish ladders, and (c) the time required to ascend the ladders. A statistical analysis of the preencroachment tagging was employed to determine adequate sample sizes and release

[4] French and Wahle also tagged in 1956, but because the tagged fish were released in a different manner and at different locations than in any other year, the 1956 experiments were excluded from our comparisons.

frequencies needed in postencroachment tagging to be 95% certain of detecting a change of one-half day and 99% certain of detecting a change of a full day in elapsed times, if such changes occurred between 1954-55 and 1964-65. If we assume that the basic condition of the tagged fish and the time required for tagged fish to recover from possible effects of tagging did not differ significantly between the 1954-55 and 1964-65 experiments, it follows that changes in elapsed times could be attributed to the ability of tagged fish to find and ascend the fishways. The efficiency of the fish-passage system at Rock Island Dam could thus be compared under pre- and postencroachment conditions. Although travel times were expected to be the most sensitive measure of encroachment effects, it is obvious that any significant drop in the percentage of tagged fish passing over the dam would indicate severe stress under postencroachment conditions.

It might seem unrealistic at first to assume that tagged fish recovered from the possible effects of tagging equally well in the pre- and postencroachment phases of the study. One might expect, for example, that tagged fish were released into faster moving water in 1954-55 and into slower moving water in 1964-65 and that, accordingly, the tagged fish required longer to recover from the effects of tagging in the earlier phase of the study than in the latter. If this were true, we might have ended up measuring differences in recovery time of tagged fish rather than differences in the efficiency of the Rock Island Dam fish ladders.

Although water velocities were not measured at the release sites, velocities measured in a model of Rock Island Dam (Ward, 1965)[5] were not uniformly different under postencroachment conditions than under preencroachment conditions. In fact, velocities at the measuring point nearest the right-bank release site on the simulated model were generally higher after encroachment than before. On the other hand, at the station closest to the left-bank release site, velocities were higher at lower river flows and about the same at higher flows after encroachment.

Observations made during the 1964-65 experiments revealed that large numbers of tagged fish tended to remain close to shore in protective eddies. According to French, tagged fish behaved similarly during the 1954-55 experiments.[6] These observations tend to support the assumption that tagged fish recovered from tagging equally well in 1954-55 and 1964-65.

The flooding of the lower portions of the fish ladders at Rock Island Dam by Wanapum Reservoir was not the only factor affecting fish passage that changed between 1954-55 and 1964-65. Riprap was added to the left bank of the river below the dam, and the left and center fish ladders were modified extensively. Figures 3 and 4 show Rock Island Dam before and after Wanapum Reservoir had been filled. New spill patterns designed to enhance fish passage were in effect throughout most of the 1964 and all of the 1965 tagging. The basic pattern was developed from findings of the 1958 study (Leman and Paulik, 1966) and modified slightly after experiments with the model of Rock Island Dam (Ward, 1965, see footnote 5).

METHODS AND MATERIALS

The basic experimental procedure was as follows: salmon were trapped as they passed over the left ladder, transported to the release sites approximately 300 m below Rock Island Dam on either side of the river, then tagged and released. Fish counters at the dam recorded the tags as the tagged fish passed the counting boards after reascending the ladders.

TAGGING

Two different traps were used to capture the salmon. Sockeye were captured as they entered a trap placed at the upstream edge of the counting board in the left-bank fish ladder. Chinook salmon, which would not enter this trap, had to

[5] Ward, David A. 1965. Hydraulic model studies of the Rock Island fish attraction facilities. Wash. State Univ., Pullman, Div. Ind. Res., Inst. Technol., Res. Rep. 65/9-43. Vol. I—20 p., 29 fig., Append. I-II; Vol. II—23 fig. (Processed.)

[6] Personal communication, Robert R. French, Fishery Biologist, Natl. Mar. Fish. Serv., Northwest Fish. Cent., Seattle, Wash.

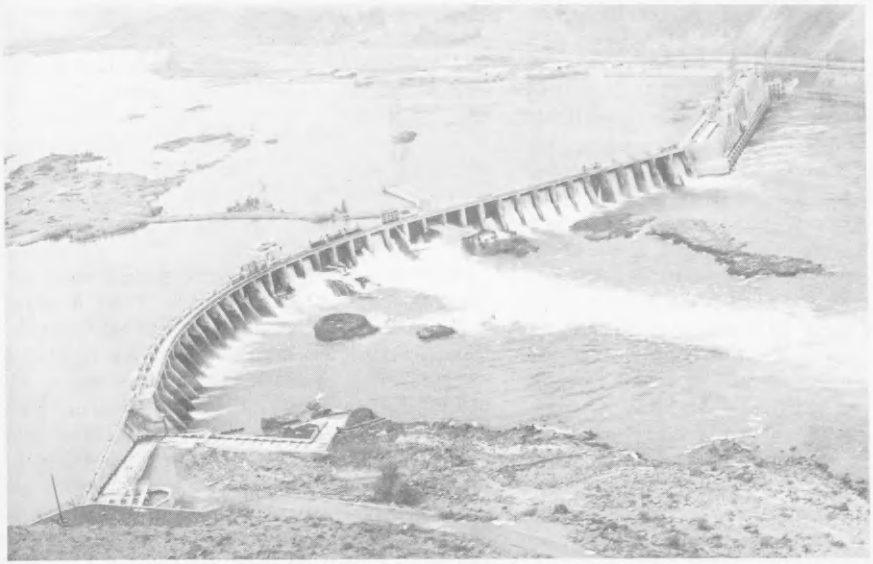

FIGURE 3.—Rock Island Dam before Wanapum Dam had been built.

FIGURE 4.—Rock Island Dam after Wanapum Dam had been built. Note how the rocks and the lower portion of the right-bank fish ladder, visible below the dam in Figure 3, have been inundated in Figure 4.

be taken in a larger floating trap positioned at the upstream end of the ladder.

A conventional 1,000-gal (3.79-m^3) tank truck transported sockeye salmon in 1964 and 1965 and chinook salmon in 1965 but was not available for the 1964 chinook salmon experiments. Instead, we used 1.2 m by 1.2 m by 1.1 m plywood boxes, equipped with aeration systems and mounted on ¾-ton (680-kg) trucks. These units were suitable for transporting fish to the adjacent left-bank release site but inadequate for moving more than seven or eight fish per unit to the opposite bank via Wenatchee, Wash.,—a 48-km trip that took about ½ hr. Because of this limitation, only one-half as many chinook salmon were released on the right bank as on the left bank in 1964.

Each batch of fish liberated was distinctively marked. Several types and colors of tags were used. Petersen plastic disks were used either alone or in combination with plastic bars and vinyl streamers. Nickel pins, inserted through the body just below the dorsal fin, provided the attachment. Tags were applied in pairs, so that the same color and type of tag showed on both sides of the fish. Tagging time seldom exceeded 30 sec per fish.

ARTIFICIAL MANIPULATION OF SPILL PATTERN, AUGUST 3-5, 1964

The spill pattern throughout most of the 1964 and 1965 tagging was developed from results of experiments at Rock Island Dam in 1958 (Leman and Paulik, 1966) with subsequent refinements from a model study in 1964 and 1965 (Ward, 1965, see footnote 5). On August 3-5, 1964, however, gates 16 to 18 (adjacent to the center ladder) were closed and gates 34, 36, and 37 (adjacent to the right-bank ladder) were opened. This departure from the recommended spill pattern was undertaken to measure its effect on the passage of tagged fish over the dam.

TAG OBSERVATION AND DATA RECORDING

Four steps were taken to insure the accuracy of the tag observations: First, hydroscopes (floating "windows") were installed over the counting boards on the right- and left-bank ladders to suppress glare and surface disturbance. Second, all fish counters were tested for color blindness. Third, samples of tags were mounted on the tally boards to facilitate instant recognition and recording of the tags. Fourth, fish counters were systematically rotated between ladders to distribute any bias by the counters between the ladders.

The gates in the fish ladders were open and the passing fish were counted 16 hr a day—5:00 AM to 9:00 PM—during these experiments. The half-day units used to measure travel times were adapted to the counting schedule. Fish observed during the same 8-hr period in which they were released were assigned a travel time of one-quarter day or 0.5 half-day. Fish released just before noon (as most were) were given a travel time of 0.5 half-day, if observed the same day, or a time of 1.0 half-day if observed the next morning. Tag observations were grouped by tag combination, ladder, and travel time in half days. Data were punched on IBM cards—one card containing the release and recovery data for each fish. The numbers of tagged salmon released below Rock Island Dam and later observed passing the dam in 1954, 1955, 1964, and 1965 are summarized in Table 1.

TABLE 1.—Numbers of salmon that were tagged and released below Rock Island Dam in 1954, 1955, 1964, and 1965, and the numbers and percentages of tagged fish that were later observed passing over the dam's fish ladders.[1]

Species of salmon	Year	Fish tagged and released below dam	Tagged fish observed passing dam	
		no.	no.	%
Spring chinook	1954	155	60	38.7
	1955	157	94	59.9
	1964	103	93	90.3
	1965	311	285	91.6
Sockeye	1954	1,485	1,176	79.2
	1955	1,176	793	67.4
	1964	951	895	94.1
	1965	679	623	91.8

[1] The numbers of spring chinook salmon released in 1954 and 1955 differ from those reported by French and Wahle (1966). They used the July 13 date suggested by Fish and Hanavan (1948) as the termination of the spring run and the beginning of the summer run. We used the scale method described by Koo and Isarankura (1967) to determine that the dates of least overlap between the two races were July 30, 1954, and July 8, 1955. We believe that our separations, based on the more recent study, are the more accurate.

TAG OBSERVATIONS AT ROCK ISLAND DAM, 1964 AND 1965

The 1964 and 1965 data are treated by species—spring chinook salmon first, followed by sockeye salmon. In a later section these data will be compared to the 1954 and 1955 results to determine the effects of encroachment of Wanapum Reservoir on fish passage at Rock Island Dam.

SPRING CHINOOK SALMON

The tag release and tag observation data for 1964 and 1965 are presented in Table 2. Included are the date and location of release, the number of fish tagged, the release area, and the number and mean travel time of tagged fish subsequently observed passing Rock Island Dam. Logarithmically transformed data are used throughout this paper for analysis of travel time; means are geometric means.

Three times as many chinook (311) were tagged in 1965 as in 1964 (103). The small number released and the short duration of the tagging period in 1964 (May 19-27) can be attributed to difficulties in completing the access roads, difficulties with the trapping and transportation systems, and a shortage of fish in the left-bank ladder—the ladder where the trap was located. Tagging was from May 16 to June 9, 1965. The 1965 data are grouped, somewhat arbitrarily, into five time periods.

Percentage Observed

The overall percentages of tagged chinook salmon subsequently observed passing over Rock Island Dam were 90.3 in 1964 and 91.6 in 1965. Variability among the release groups was high, ranging from 67 to 129% in 1964 and 60 to 115% in 1965. It is noteworthy that the number observed exceeded the number released for 6 of the 24 releases over the two tagging seasons.

TABLE 2.—Numbers of chinook salmon that were tagged, released below Rock Island Dam and the numbers and mean travel times of tagged fish that were later observed passing over the dam's fish ladders, 1964 and 1965.

			Number of fish tagged and released below dam		Number and mean travel time in half-days of tagged fish observed passing dam							
					Left ladder		Center ladder		Right ladder		Total[1]	
Year	Period	Date	Left bank	Right bank	No.	Travel time	No.	Travel time	No.	Travel time	No.	Travel time
1964		May 19	17	--	10	14.8	5	16.8	7	8.5	22	12.8
		May 19	--	15	6	6.0	6	8.7	1	4.0	13	6.9
		May 20	13	--	7	13.2	6	13.4	2	14.8	15	13.5
		May 20	--	17	6	18.1	3	5.3	4	6.6	13	10.0
		May 21	27	--	9	10.5	7	4.2	4	8.1	20	7.2
		May 21	--	5	1	7.0	3	12.6	0	--	4	10.9
		May 27	9	--	4	9.9	0	--	2	8.7	6	9.5
1965		May 16	5	--	1	2.5	3	3.4	1	2.5	5	3.0
	I	May 18	5	--	2	11.5	2	4.0	1	2.0	5	5.3
		May 21	--	19	12	6.8	4	2.7	3	4.0	19	5.1
		May 22	41	--	33	5.4	9	15.8	5	5.7	47	6.6
		May 23	--	11	8	7.0	3	5.2	0	--	11	6.4
		May 24	9	--	4	4.7	0	--	2	2.5	6	3.8
	II	May 24	--	25	17	7.7	6	4.7	3	2.5	26	6.0
		May 25	8	--	5	3.1	2	22.5	2	12.5	9	6.6
		May 26	15	--	8	4.8	0	--	1	0.5	9	3.7
	III	May 27	--	30	23	8.2	4	5.9	5	3.9	32	7.0
		May 28	28	--	16	9.1	4	15.5	5	3.7	25	8.3
	IV	May 31	21	--	10	6.7	2	5.2	2	6.5	14	6.5
		June 1	--	27	14	6.4	4	4.1	4	2.4	22	4.9
	V	June 4	10	--	5	2.7	3	8.0	0	--	8	4.1
		June 4	--	22	11	6.9	2	6.6	5	2.3	18	5.0
	VI	June 8	--	22	12	3.9	3	5.1	5	3.2	20	3.9
		June 9	13	--	8	6.5	1	20.5	0	--	9	7.3

[1] The total number observed may exceed the number tagged. See text (p. 132) for explanation.

Possible explanations include the misidentification of tags by the counters and multiple observations of the same tagged fish that passed over the dam, fell back, and survived to pass over the dam again. The "falling back" of salmon over dams is a frequent occurrence on the Columbia River (Johnson, 1965),[7] although recent studies[8] have shown the magnitude of such fallback is not large (usually less than 5%).

The percentages of tagged fish recovered by release location (releases pooled by location within years) were not consistent for the 2 years. In 1964 the percentage of tagged fish released on the left bank and subsequently observed exceeded that of the right bank—95.5 to 81.1. In 1965 the comparable percentages were 88.4 and 94.9, respectively.

Distribution by Ladder

Of the tagged fish sighted in 1964, nearly one-half (46.2%) chose the left ladder; the center and right ladders lured 32.3 and 21.5%, respectively. In 1965, 66.3% chose the left ladder, 18.2% the center ladder, and 15.4% the right ladder. Distribution between ladders was basically the same for each release site within, but not between, years. The percentages observed in the left ladder were 47.6 and 43.3 for the left- and right-bank releases in 1964 but considerably higher (67.2 and 65.5) for fish released from the left and right banks, respectively, in 1965. However, in both years similar percentages of the fish not using the left ladder chose the center ladder (60.0 in 1964 and 54.1 in 1965).

Between-period comparisons are possible for 1965 only when the percentage of tagged fish using the left-bank ladder remained very consistent from period to period, varying only from 61.5 to 69.0.

[7] Johnson, James H. 1965. Fallback of adult chinook salmon at Ice Harbor Dam spillway, May 1964. Final Report to U.S. Army Corps of Engineers for Research Contract No. DA-45-164-CIVENG-63-286. Bur. Commer. Fish., Fish-Passage Research Program, Seattle, Wash., 16 p. (Processed.)

[8] Personal communication with Charles Junge of the Oregon Fish Commission with regard to experiments with tagged chinook salmon at Bonneville Dam during 1970.

Travel Time from Release to Observation in Fish Ladders

Travel times—by date of release, release location, and ladder in which the tagged spring chinook salmon were sighted—are presented in Table 2. Because of the small numbers of fish involved in the 1964 tests, their value is limited. The 1965 experiments provided the most sensitive analysis of the time required for tagged fish to pass over Rock Island Dam under encroachment conditions.

Results of analysis of variance tests of the hypothesis of no difference in mean travel time between fish released on the right and left banks in 1965 are summarized in Table 3. Regardless of how the data were grouped—whether travel times of the right-bank and the left-bank releases were compared period by period, whether adjacent periods were combined, or whether all periods were pooled—no statistically significant differences were found. It is noteworthy, however, that the mean passage time for fish released from the right-bank site was less than for fish released at the left-bank site. Thus, fish released from the right bank were finding and passing over the ladders at least as fast as, if not faster than, those released from the left bank.

TABLE 3.—Analysis of variance tests of the hypothesis that spring chinook salmon, tagged and released on the left bank below Rock Island Dam in 1965, traveled over the Rock Island Dam fish ladders equally as fast as fish released on the right bank below the dam.

Periods	Mean travel time in half-days, all ladders combined		*F*-statistics (1 and 268 df)
	Left-bank releases	Right-bank releases	
I	6.081	5.130	0.32 N.S.[1]
II	4.630	6.159	0.93 N.S.
III	8.249	7.009	0.29 N.S.
IV	6.454	4.940	0.48 N.S.
V	4.054	5.048	0.21 N.S.
VI	7.342	3.855	2.03 N.S.
			F-statistics (1 and 279 df)
I and II	5.609	5.789	0.03 N.S.
III and IV	7.553	6.078	0.64 N.S.
V and VI	5.553	4.380	0.50 N.S.
			F-statistics (1 and 283 df)
I-VI	6.097	5.486	0.63 N.S.

[1] N.S. = Not significant.

TABLE 4.—Analysis of variance tests of the hypothesis that spring chinook salmon, tagged and released below Rock Island Dam in 1965, traveled over the right fish ladder at Rock Island Dam equally as fast as those traveling over the left and center ladders.

Ladders compared	Mean travel time in half days, release areas combined			*F*-statistics[1] (1 and 268 df)
	Left ladder	Center ladder	Right ladder	
Right vs. left	6.210	--	3.396	10.60**
Right vs. center	--	6.929	3.396	9.86**

[1] ** = Highly significant at the 0.01 level, reject hypothesis of equal travel times, and conclude that travel time was significantly less through the right ladder.

We also analyzed the 1965 data on a ladder by ladder basis. Although the data, even when compared on a period by period basis, are too limited to provide a sensitive comparison of the mean passage times between fish using the different ladders, they did reveal that in every period fish moved over the right ladder faster than over either the center or left ladder. Mean passage times for right ladder versus the left ladder and right ladder versus the center ladder (all periods and both release sites pooled) are compared in Table 4.[9] The data have been adjusted for simultaneous tests according to the method described by Dunn (1961). The differences shown in Table 4 are highly significant. Thus the hypothesis that spring chinook salmon traveled from the tagging sites over the right ladder equally as fast as over the left ladder is strongly rejected as is the same hypothesis for the right versus the center ladder. In both cases the mean passage times are significantly less for fish using the right ladder. This means that ladder choice was the only observed factor clearly affecting passage time. Similar trends were noted in 1964. Mean passage time over the right ladder was less than for either the left or center ladders.

The overall travel time in 1965 (5.8 half-days) was shown by an analysis of variance test to be significantly less than that of 1964 (9.8 half-days). The *F*-value for this test was 17.72 with 1 and 165 degrees of freedom.

[9] Because the passage of fish over the right-bank fish ladder had been a source of controversy among fishery biologists, we directed special attention to the right-bank ladder in the present study.

SOCKEYE SALMON

Fewer sockeye salmon were tagged in 1965 than in 1964. Analysis of the 1964 data revealed that the precision desired could still be achieved if sample sizes were reduced from 100 to 75 fish per release in each year. The tagging season was divided into five periods. With one exception, each of these periods contained releases from the left and right banks. During period IV in 1965, both releases were from the left bank.

Tagging was from July 15 to August 5 in 1964 and from July 14 to August 4 in 1965. Tag release and tag observation data are presented in Table 5.

Percentage Observed

The percentages of tagged sockeye from individual releases observed passing Rock Island Dam were similar for 1964 and 1965. The percentage ranged from 84.3 to 120.8 in 1964 and from 81.2 to 98.8 in 1965. Overall, 94.1% of the tagged fish were observed in 1964 and 91.8% in 1965. Percentages observed from left-bank releases were not significantly different from those released on the right bank in either year—94.8 (left bank) versus 93.3 (right bank) in 1964 and 91.5 (left bank) versus 92.0 (right bank) in 1965.

Distribution by Ladder

Distribution by ladder was similar in both years. Of the tagged fish sighted, 55.6% used the left ladder in 1964 and 53.1% in 1965. The center ladder took 20.7 and 23.6% and the right ladder 23.7 and 23.3% in the 2 years, respectively. For the left- and right-bank releases, respectively, the percentages using the left ladder were 54.1 and 57.4 in 1964. Comparable percentages were 55.4 and 50.7 in 1965. Fish not choosing the left ladder were fairly evenly distributed between the center and right ladders in both years.

The between-period consistency of the percentage of tagged sockeye salmon using the preferred left ladder was less evident than for chinook salmon. For sockeye salmon, the

TABLE 5.—Numbers of sockeye salmon that were tagged, released below Rock Island Dam and the numbers, and mean travel times of tagged fish that were later observed passing over the dam's fish ladders, 1964 and 1965.

			Number of fish tagged and released below dam		Number and mean travel time in half-days of tagged fish observed passing dam							
					Left ladder		Center ladder		Right ladder		Total[1]	
Year	Period	Date	Left bank	Right bank	No.	Travel time	No.	Travel time	No.	Travel time	No.	Travel time
1964	I	July 15	76	--	21	2.7	16	2.2	40	2.4	77	2.4
		July 16	24	--	16	2.2	9	1.9	7	2.0	29	2.1
		July 17	--	113	48	5.9	29	4.8	29	6.8	106	5.8
	II	July 21	--	70	35	4.9	8	4.9	16	3.0	59	4.3
		July 22	104	--	59	3.4	16	2.8	15	4.1	90	3.4
		July 23	--	89	48	5.7	20	3.3	16	4.8	84	4.8
	III	July 28	92	--	45	1.6	25	1.3	19	3.2	89	1.7
		July 30	--	80	56	5.0	20	3.3	11	5.5	87	4.6
	IV	July 31	85	--	53	2.3	16	3.4	13	3.3	82	2.7
		August 3	70	--	38	4.4	10	2.8	15	5.6	63	4.4
	V	August 4	--	96	53	4.8	13	3.3	16	5.6	82	4.6
		August 5	52	--	26	4.1	6	2.8	15	3.1	47	3.6
1965	I	July 14	71	--	38	3.1	8	3.8	23	2.4	69	2.9
		July 15	--	68	38	4.2	9	2.3	20	3.5	67	3.7
	II	July 19	81	--	51	4.6	7	4.2	22	4.7	80	4.6
		July 20	--	76	43	4.1	6	2.9	23	2.9	72	3.5
	III	July 27	75	--	36	3.7	19	2.8	13	3.4	68	3.4
		July 28	--	75	28	2.5	28	2.1	16	1.9	72	2.2
	IV	July 29	69	--	25	4.3	18	4.5	13	4.1	56	4.3
		July 30	--	66	25	2.0	19	2.7	13	2.6	57	2.4
	V	August 3	60	--	29	2.0	19	3.0	1	2.5	49	2.4
		August 4	--	38	18	3.1	14	3.5	1	2.0	33	3.3

[1] The total number observed may exceed the number tagged. See text (p. 132) for explanation.

percentage varied from 40.1 to 62.8 in 1964 and from 44.2 to 61.8 in 1965. For chinook salmon, the range was 61.5 to 69.0% in 1965, the only year in which adequate data were obtained.

Travel Time from Release to Observation in Fish Ladders

Travel time by date of release, release location, and ladder for the 1964 and 1965 experiments are presented in Table 5. Following analysis of the 1964 data, we will examine the 1965 experiments (p. 135).

Analysis of variance tests of the hypothesis of no difference in travel time between left- and right-bank releases (all ladders combined) are given in Table 6. Because there were no releases from the right bank in period IV, the test compares the two left-bank releases. Within-release group variances were pooled to form an overall pooled estimate of the variance with 883 degrees of freedom. Because the mean travel times did not differ significantly between the July 15 and 16 left-bank releases, these releases were combined. The July 21 and 23 right-bank releases were similarly tested and combined. Note that in periods I to III, travel times for the left-bank releases were significantly less than

TABLE 6.—Analysis of variance tests of the hypothesis that sockeye salmon, tagged and released on the left bank below Rock Island Dam in 1964, traveled over the Rock Island Dam fish ladders equally as fast as fish released on the right bank; the testing period IV involves two left-bank releases.

Period	Release locations compared	Mean travel time in half-days, all ladders combined		F-statistics[1] (1 and 883 df)
		Left bank	Right bank	
I	Left vs. right	2.331	5.787	72.95 **
II	Left vs. right	3.394	4.617	8.71 **
III	Left vs. right	1.746	4.619	69.38 **
IV	Left (July 31) vs. Left (Aug. 3)	2.651 4.350	--	14.55 **
V	Left vs. right	4.628	3.604	3.11 N.S.

[1] ** = Highly significant at the 0.01 level, reject hypothesis of equal travel times, and conclude that travel time was significantly less for fish released from one bank than for those released on the other bank.
N.S. = Not significant at the 0.05 level, accept hypothesis of equal travel times.

for the right-bank releases. In period IV when both releases were from the left bank, the travel time of fish released on August 3 was significantly higher than that of fish released on July 31. Differences were not significant in period V when fish were released from both left and right banks.

There is little doubt then that in periods I to III (when the spill pattern recommended by the study group was in operation), fish released from the left bank were finding the ladders and traveling over the dam faster than those released on the right bank. During the last two periods (V and VI), the flows were intentionally switched from the center to the right and back again. The effects of this change on fish passage are discussed in greater detail in a later section.

Further examination of Table 5 reveals two additional characteristics about the movement of tagged sockeye salmon over Rock Island Dam in 1964. First is the consistency of the relative passage times between ladders for fish from a given tag release. This means that regardless of how rapidly or slowly fish from a particular release moved, they did so more or less uniformly at all three ladders. Spring chinook salmon (Table 2) varied much more than did the sockeye in this respect. Second, in five of six comparisons fish released on the left bank negotiated the right-bank fish ladder faster than did fish released on the right bank. Considered jointly, these two features suggest that sockeye were capable of rapid lateral movement in the area downstream from the dam and that the passage of fish released on the right bank was somehow delayed whether they chose the left, center, or even the adjacent right-bank ladder.

Table 7 depicts the travel times by period and ladder, ignoring release sites. Corresponding statistical tests of the hypothesis of no difference in travel times between the right and center and between right and left fish ladders are included. For these tests, a pooled estimate of the error variance with 880 degrees of freedom was computed from within-ladder variances for the 15 groups. Because we tested left versus right and center versus right ladders simultaneously, using the same within-period data, we modified the *t*-test to control the type I error according to the method suggested by Dunn (1961).

Only one difference is significant. In period III, the mean passage time through the center ladder was less than through the right ladder. In general, however, passage time does not appear to be influenced by the ladder chosen.

Analysis of variance tests of the hypothesis of no difference in travel time between fish released on the right and left banks (all ladders combined) in 1965 are presented in Table 8. The conclusions from these tests are mixed. Fish traveled over the dam faster from the left-bank release site than from the right-bank release

TABLE 7.—Analysis of variance tests of the hypothesis that sockeye salmon, tagged and relased below Rock Island Dam in 1964, traveled over the right fish ladder at Rock Island Dam equally as fast as those traveling over the left and center ladders.

Period	Ladders compared	Mean travel time in half-days, release areas combined			*t*-statistics[1]	Degrees of freedom
		Left ladder	Center ladder	Right ladder		
I	Left vs. right	4.018	--	3.530	0.981 N.S.	(1, 159)
	Center vs. right	--	3.358	3.530	−0.329 N.S.	(1, 125)
II	Left vs. right	4.453	--	3.887	0.967 N.S.	(1, 187)
	Center vs. right	--	3.324	3.887	−0.893 N.S.	(1, 89)
III	Left vs. right	2.989	--	3.874	−1.494 N.S.	(1, 129)
	Center vs. right	--	2.014	3.874	−3.321 *	(1, 73)
IV	Left vs. right	3.042	--	4.399	−2.043 N.S.	(1, 117)
	Center vs. right	--	3.155	4.399	−1.461 N.S.	(1, 52)
V	Left vs. right	4.547	--	4.211	0.434 N.S.	(1, 108)
	Center vs. right	--	3.132	4.211	−1.215 N.S.	(1, 48)

[1] N.S. = Not significant at the 0.05 level, accept hypothesis of equal travel times.
* = Significant at the 0.05 level, reject hypothesis of equal travel times, and conclude that travel time through the center ladder was significantly less than through the right ladder.

TABLE 8.—Analysis of variance tests of the hypothesis that sockeye salmon, tagged and released on the left bank below Rock Island Dam in 1965, traveled over the Rock Island Dam fish ladders equally as fast as fish released on the right bank.

Period	Mean travel time in half-days, all ladders combined		F-statistics[1] (1 and 613 df)
	Left-bank releases	Right-bank releases	
I	2.943	3.674	3.239 N.S.
II	4.589	3.543	4.915 *
III	3.374	2.182	12.867 **
IV	2.363	4.319	25.511 **
V	2.368	3.251	3.841 *

[1] N.S. = Not significant at the 0.05 level, accept hypothesis of equal travel times.
* = Significant at the 0.05 level, reject hypothesis of equal travel times, and conclude that travel time for fish released on one bank was significantly less than for fish released on the other bank.
** = Significant at the 0.01 level, reject hypothesis, and conclude as above.

site in period I but not significantly so. In periods II and III, fish released on the right bank moved over the dam significantly faster than their left-bank counterparts. In periods IV and V, statistically significant differences were found only in the other direction, e.g., left-bank releases were faster than right-bank releases.

Thus, there is no clear superiority of one release location over the other. The effect of release location on relative and absolute travel times changed from period to period. In contrast, tagged sockeye salmon released from the left-bank site in 1964, before the spill was intentionally modified, moved past the dam faster than their right-bank counterparts. The main difference between the 2 years seems to be the decreased passage time for the right-bank releases of 1965 which, for every comparable period, moved over the dam faster than their 1964 counterparts.

Overall travel times (3.6 half-days in 1964 and 3.2 half-days in 1965) did not differ significantly despite the better performance by the right-bank releases.

Next, it is appropriate to examine the effect of ladder choice on mean travel time in 1965 by period and with release areas pooled. The basic data and the corresponding tests of significance are given in Table 9. No significant differences were found. Ladder choice did not appear to influence travel time. The same result was noted in 1964.

SPILL PATTERN MANIPULATION

On August 3, 4, and 5, 1964, spill was shifted from gates adjacent to the center ladder to the gate on the far right side of the dam. During this 3-day period, two groups of tagged fish (August 3 and 5) were released from the left bank and one (August 4) from the right bank. We will consider the left-bank releases first. The release of August 3 was subjected to 3 days of the modified spill condition, whereas the release of August 5 was subjected to 1 day of the same condition. The left-bank release of July 31 provided a crude "control" (no effect of modified

TABLE 9.—Analysis of variance tests of the hypothesis that sockeye salmon, tagged and released below Rock Island Dam in 1965, traveled over the right fish ladder at Rock Island Dam equally as fast as those using the left and center ladders.

Period	Ladders compared	Mean travel time in half-days, release areas combined			F-statistics[1]	Degrees of freedom
		Left ladder	Center ladder	Right ladder		
I	Right vs. left	3.642	--	2.868	3.051 N.S.	(1, 117)
	Right vs. center	--	2.906	2.868	0.004 N.S.	(1, 58)
II	Right vs. left	4.354	--	3.639	1.903 N.S.	(1, 137)
	Right vs. center	--	3.577	3.639	0.006 N.S.	(1, 56)
III	Right vs. left	3.096	--	2.502	1.766 N.S.	(1, 91)
	Right vs. center	--	2.340	2.502	0.155 N.S.	(1, 74)
IV	Right vs. left	2.946	--	3.288	0.402 N.S.	(1, 74)
	Right vs. center	--	3.464	3.288	0.080 N.S.	(1, 71)
V	Right vs. left	2.400	--	2.236	0.019 N.S.	(1, 47)
	Right vs. center	--	3.201	2.236	0.472 N.S.	(1, 33)

[1] N.S. = Not significant at the 0.05 level, accept hypothesis of equal travel times.

spill) for the two "experimental" releases on August 3 and 5.

The percentages of the tagged fish observed in the right ladder were 15.9, 23.8, and 31.9 for the releases of July 31 (0-day modified spill), August 3 (3-day modified spill), and August 5 (1-day modified spill), respectively. Comparable percentages were 19.5, 15.9, and 12.8 for the center ladder and 64.6, 60.3, and 55.3 for the left ladder. Travel times for the three releases averaged 2.7, 4.4, and 3.6 half-days respectively. Thus, it appears that spilling from the right side tended to attract fish released on the left bank to the right ladder but at the expense of increasing overall travel time.

The change in the spill pattern did not have a significant effect on tagged fish released on the right bank. For the July 30 "control" release, mean travel time was 4.6 half-days; for the August 4 "experimental" release it was 4.6 half-days. Slightly more fish from the August 4 release (19.5%) were attracted to the right ladder than from the July 30 release (12.6%).

Most striking is the similarity between the left-bank release of August 3 and the right-bank release of August 4. The percentages of tagged fish using various ladders for the releases of August 3 and 4 were: (see Table 5) left, 60.3 and 64.6; center, 15.9 and 15.9; and right, 23.8 and 19.5. Overall travel times were 4.4 and 4.6 half-days. Travel times by ladder were similar —4.4 and 4.8 half-days for the left, 2.8 and 3.3 for the center, and 5.6 and 5.6 for the right ladder.

In summary, the departure from the basic spill pattern tended to attract fish to the right-bank ladder, especially those released on the left bank and in so doing, increased the overall travel time. These experiments support the efficacy of the basic spill pattern as compared to the other pattern tested.

COMPARISON OF PREENCROACHMENT AND POSTENCROACHMENT TAGGING STUDIES

The effect of the encroachment of Wanapum Reservoir on fish passage at Rock Island Dam is best measured by comparing the results of the pre- and postencroachment tagging studies. We shall consider spring chinook salmon first, followed by sockeye salmon. Three measurements—percentage observed, distribution by ladder, and travel time—provide the basis of our analysis.

SPRING CHINOOK SALMON

The results of the 1954 and 1955 tagging studies with spring chinook salmon are presented in Tables 10 and 11. Comparable data for 1964 and 1965 are in Table 2.

Percentage Observed

The overall percentages of tagged spring chinook salmon observed passing Rock Island Dam were 38.7 and 59.9 in 1954 and 1955; they were 90.3 and 91.6 in 1964 and 1965. Although some of the significant increase may represent better tag retention or increased survival brought about by improved conditions for fish passage during the postencroachment study, it is likely that the precautions we took to improve the tag observations also were important.

It is interesting to note that the greatest increase occurred for fish released from the right-bank site. In 1954 and 1955, sightings from right-bank releases were only 37.5 and 51.9%, whereas in the postencroachment years—1964 and 1965—they were 81.1 and 94.9%. Few fish were released on the left bank in 1954, but the increase in the percentage of tagged fish observed for the other years (from 77.6 in 1955 to 95.5 and 88.4 in 1964 and 1965) while significant, is not as dramatic as for the right-bank releases.

Distribution by Ladder

The percentages of tagged spring chinook salmon in the left-bank fish ladder were 61.7, 74.5, 46.2, and 66.3 in 1954, 1955, 1964, and 1965, respectively. For the right ladder the percentages were 25.0, 16.0, 21.5, and 15.4 for the 4 years, respectively. This means that 13.3% used the center ladder in 1954, 9.6% in 1955, 32.3% in 1964, and 18.2% in 1965. Thus, there was no

TABLE 10.—Tag release and observation data for spring chinook salmon seen passing over fish ladders at Rock Island Dam, 1954 and 1955.[1]

Date	Tagging location	Number of fish tagged and released	Number of tagged fish observed			
			Left ladder	Center ladder	Right ladder	Total
1954						
June 23-25	Right bank	26	6	3	7	16
June 29-July 2	Right bank	36	5	2	2	9
July 7-9	Right bank	57	7	1	5	13
July 13	Right bank	26	15	2	0	17
July 16-22	Left bank	3	3	0	0	3
July 29-30	Right bank	7	1	0	1	2
1955						
June 7-9	Left bank	8	3	0	1	4
	Right bank	14	7	1	1	9
June 14-15	Right bank	13	7	1	2	10
June 17-21	Left bank	9	10	0	2	12
	Right bank	19	6	1	2	9
June 28-29	Right bank	15	10	0	0	10
June 30-July 1	Right bank	19	3	2	2	7
July 5-6	Left bank	17	8	3	1	12
July 7-8	Right bank	43	16	1	4	21

[1] The total number observed may exceed the number tagged. See text (p. 132) for explanation.

TABLE 11.—Travel time of tagged spring chinook salmon from tagging areas below Rock Island Dam to the Rock Island fish ladders, 1954 and 1955.

Date	Tagging location	Mean travel time in half-days, all ladders combined
1954		
June 23-25	Right bank	12.3
June 29-July 2	Right bank	7.4
July 7-9	Right bank	14.9
July 13	Right bank	13.8
July 16-22	Left bank	15.8
July 29-30	Right bank	10.6
1955		
June 7-9	Left bank	6.5
	Right bank	19.4
June 14-15	Right bank	12.4
June 17-21	Left bank	24.2
	Right bank	21.8
June 28-29	Left bank	20.3
June 30-July 1	Right bank	9.2
July 5-6	Left bank	19.6
July 7-8	Right bank	12.8

marked and repeatable difference in distribution by ladder between the postencroachment years, 1964 and 1965, and the preencroachment years, 1954 and 1955. The center ladder took a disproportionate share of the fish in 1964 (at the expense of the left ladder), but this was less pronounced in 1965.

Travel Time from Release to Observation in Fish Ladders

Apparently no large-scale mortalities and no great losses of tags were caused by encroachment (these assumptions are supported by the high percentages of tagged fish subsequently seen passing Rock Island Dam). The overall effect of encroachment is then best measured by comparing the travel times between the pre- and postencroachment tagging studies. Although we have already shown that the 1965 travel time (5.8 half-days) was significantly less than the 1964 travel time (9.0 half-days), this difference does not overshadow the fact that both values are well below the comparable figures (12.4 and 16.0 half-days) for 1954 and 1955, respectively. We can only conclude that travel time of spring chinook has decreased markedly since encroachment.

SOCKEYE SALMON

Results of the 1954 and 1955 tagging studies with sockeye salmon are given in Table 12. Comparable data for 1964 and 1965 are presented in Table 5.

TABLE 12.—Tag releases, tag observations, and travel times for sockeye salmon seen passing over fish ladders at Rock Island Dam, 1954 and 1955.

Period	Date	Tagging location	Number of fish tagged and released	Number of tagged fish observed[1]	Mean travel time in half-days
1954					
I	July 7-8	Right bank	22	22	23.3
II	July 16, 20	Left bank	119	168	12.5
	July 21-22	Right bank	155	151	10.1
III	July 22-23	Left bank	272	196	8.4
	July 27-29	Right bank	146	75	7.7
IV	July 28-30	Left bank	246	111	7.3
	August 3	Right bank	89	80	6.6
V	August 6-12	Left bank	174	128	4.8
	August 5-12	Right bank	262	245	6.4
1955					
I	July 19-20	Right bank	123	118	7.3
II	July 21	Left bank	59	46	7.0
	July 22	Right bank	46	6	14.9
III	July 26-29	Left bank	298	224	7.0
	July 26-28	Right bank	227	151	5.2
IV	August 2-3	Left bank	129	119	7.1
	August 2	Right bank	24	12	3.8
V	August 5-10	Left bank	93	38	7.1
	August 4-11	Right bank	177	79	7.5

[1] The number observed may exceed the number tagged. See text (p. 132) for explanation.

Percentage Observed

The overall percentages of tagged sockeye salmon observed passing Rock Island Dam in 1964 and 1965 (94.1 and 91.8, respectively) were significantly higher than those recorded in 1954 and 1955 (79.2 and 67.4). A similar change was noted for chinook salmon. As we mentioned earlier in discussing the results with chinook salmon, two factors—increased tag retention and improved facilities for observing and reporting tagged fish—probably contributed to the increased percentages of tagged fish that were observed. Unlike chinook salmon, for which a greater part of the increased percentage of fish sighted could be attributed to fish released on the right bank, the improvement in sockeye salmon was of the same magnitude for releases made on both banks.

Distribution by Ladder

Percentages of tagged sockeye salmon in the left ladder were 55.3, 64.3, 55.6, and 53.1 in 1954, 1955, 1964, and 1965, respectively. For the right ladder, the percentages were 13.2, 12.4, 23.7, and 23.3; for the center ladder they were 31.5, 23.3, 20.7, and 23.6. As with chinook salmon then, the distribution of tagged sockeye salmon by ladder in postencroachment years, 1964 and 1965, did not differ significantly or at least consistently so from that observed in preencroachment years, 1954 and 1955.

Travel Time from Release to Observation in Fish Ladders

Comparisons of the mean travel times by period and area of release for 1954 versus 1964 and 1965 and for 1955 versus 1964 and 1965 are presented in Figure 5. On only 1 of 34 occasions was the travel time in the preencroachment tagging year less than for the corresponding postencroachment tagging year. The difference was not significant.

As with chinook salmon then, we found the time required by tagged sockeye salmon to pass the fish ladders at Rock Island Dam was considerably less after the onset of encroachment than before.

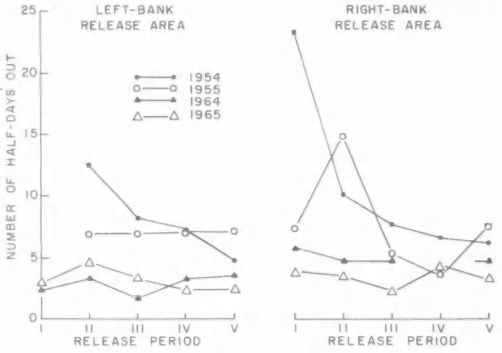

FIGURE 5.—Time required for tagged sockeye salmon to move over the Rock Island Dam fish ladders from the tagging areas below the dam, 1954, 1955, 1964, and 1965.

SUMMARY AND CONCLUSIONS

The lower portions of the fish ladders at Rock Island Dam were flooded by the reservoir of Wanapum Dam. At the direction of the Federal Power Commission, the fish ladders were modified to maintain or enhance fish passage and a study was developed to evaluate the adequacy of the modifications.

In 1964 and 1965 over 2,000 spring chinook and sockeye salmon were tagged and released below Rock Island Dam; their subsequent movement over the fish ladders was noted. Three features—travel time, the percentage of tagged fish observed, and the distribution of tagged fish by ladder—were compared with data obtained in a similar tagging study in 1954 and 1955.

Results clearly indicate that the fish passage over Rock Island Dam was better in 1964 and 1965 than in 1954 and 1955. Travel times were significantly shorter and higher percentages of tagged fish were sighted passing over the ladders under postencroachment conditions.

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SCALE FEATURES OF SOCKEYE SALMON FROM ASIAN AND NORTH AMERICAN COASTAL REGIONS

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ABSTRACT

Photographic plates of sections of sockeye salmon scales, with descriptions, and frequency tables of the number of circuli in the freshwater and first ocean zones illustrate the variations in scale features of fish over the range of the species in coastal regions of Asia and North America. Suggestions are also given for using these data to determine the geographical origin of sockeye salmon taken in offshore areas of the North Pacific Ocean and adjacent waters.

Sockeye salmon (*Oncorhynchus nerka*) are valuable food fish of the Bering Sea and the northern part of the North Pacific Ocean. They spawn in coastal streams of Asia and North America but spend a portion of their lives feeding in oceanic areas. Upon the onset of sexual maturity, they migrate from the ocean, enter their natal streams, spawn, and then die. Because sockeye return to natal streams to spawn, the species is divided into hundreds of individual populations (each from its own geographical area), which are self-reproducing units or "stocks."

A major goal in fisheries research and management of the sockeye salmon resource is to obtain enough spawning fish within each stream to provide the maximum catch to the fishery and to insure the perpetuation of each stock. This goal is difficult to attain in fishing areas where management agencies are uncertain of the geographic area of origin of the stocks of fish that are being caught. Consequently, methods for determining the area of origin of sockeye salmon taken beyond their natal streams are needed.

A number of methods have been used to determine the area of origin of sockeye salmon taken in offshore and coastal areas. These include morphological studies (Fukuhara et al., 1962; Landrum and Dark, 1968), parasitological studies (Margolis, 1963), serological studies (Ridgway, Klontz, and Matsumoto, 1962), tagging studies (Hartt, 1962, 1966; Kondo et al., 1965), and scale studies (Krogius, 1958; Kubo, 1958[2]; Kubo and Kosaka, 1959[3]; Henry, 1961; Mosher, Anas, and Liscom, 1961; and Mosher, 1963, 1968). Scale studies have become one of the most popular and successful methods; scale features, for example, are routinely used by investigators of the International Pacific Salmon Fisheries Commission as one element in a technique to determine the natal streams of sockeye taken near the mouth of the Fraser River and are also routinely used by investigators of the National Marine Fisheries Service (NMFS, formerly the Bureau of Commercial Fisheries) to determine continent of origin of sockeye salmon taken in the Bering Sea and the central North Pacific Ocean.

No detailed information, however, has been published on the variations in scale features among fish from different spawning regions along the Asian and North American coasts. Krogius (1958) specifically mentioned the need for an atlas illustrating scales from different

[1] National Marine Fisheries Service, Northwest Fisheries Center, 2725 Montlake Boulevard East, Seattle, WA 98102.

[2] Kubo, T. 1958. Study of sockeye salmon stocks by means of the growth pattern of scales (preliminary report). Fac. Fish., Hokkaido Univ. (Hakodate). Part I - 15 p. of Japanese text; Part II - 2 pl., 16 fig. in English. (Transl. of Part I, Int. North Pac. Fish. Comm. Doc. 206), 9 p. (Processed.)

[3] Kubo, T., and J. Kosaka. 1959. A study of 5_3 age group red salmon stocks by scale growth formula [in Japanese with English abst., headings, tables, and fig. legends.] Suisan cho (Fisheries Agency of Japan), (Int. North Pac. Fish. Comm. Doc. 326), 27 p. (Processed.)

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areas and included in her paper were many pictures of scales of sockeye salmon of Asian stocks. A photographic atlas of sockeye salmon scales (Mosher, 1968) was the first step in determining racial origins, and it should be available for reference when the present paper is studied.

The purpose of this paper is to show variations in age and scale characteristics among adult fish from various coastal areas over the range of the species so that workers planning to collect and analyze scale data to determine origin of sockeye taken at sea and in coastal waters are informed about scale features that are linked to various geographic localities.

This report consists of two principal parts. The first comprises (1) photographs of sections of scales of adult sockeye salmon, as plates, for each freshwater age group from various areas over the range of the species; (2) frequency tables of the number of circuli in the freshwater and first ocean zones for fish taken from the various areas; and (3) descriptions of the scales of sockeye salmon from the various areas. The second part is concerned with the selection of scale features for the determination of the origin of fish taken in offshore waters.

METHODS AND MATERIALS

In the preparation of this paper I was concerned with (1) the selection of scale samples of fish from various geographical areas, (2) the selection of scale features that are linked to various stocks or geographical areas, and (3) the method of preparation of plates from photographs of selected sockeye scales. I have discussed each of these items separately.

SELECTION OF SCALE SAMPLES OF FISH FROM VARIOUS GEOGRAPHICAL AREAS

An important consideration in deciding which stocks of sockeye salmon to include in this paper was the relative number of fish produced in the various localities over the range of the species shown in Figure 1. Study of catch data seems to be the best way to determine the most abundant stocks because the catch is roughly proportional to the production of fish in an area. Table 1 shows the average catch for the 3 years, 1966-68, the statistics for which are complete for Asia

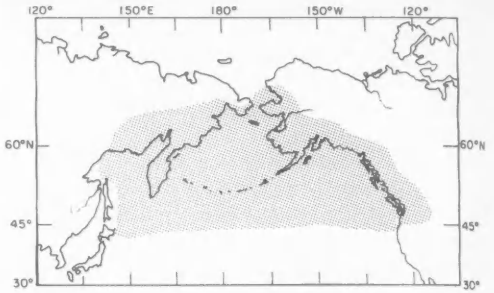

FIGURE 1.—Approximate range of sockeye salmon in and around the North Pacific Ocean and adjacent seas. The distribution in the northern Bering and Chukchi Seas was estimated to include the northernmost known spawning streams on both continents. Sockeye salmon may be found in many streams within the range shown, but in only a few streams in some areas. Atkinson et al. (1967) shows detailed maps of streams where sockeye salmon have been known in the United States. The distribution at sea varies within and between years, depending on many factors, Manzer et al. (1965), Hartt (1962, 1966), and Kondo et al. (1965). In addition to the above references, Hanamura (1966, 1967) and Aro and Shepard (1967) were also sources of data for this figure.

TABLE 1.—Sockeye salmon catch, average of 1966-68.

Area	Thousands of fish	Metric tons
Total all areas	27,297.2	70,387.0
Asia	9,512.6	20,972.6
Japan[1]	8,527.0	17,988.6
USSR	985.6	2,984.0
North America	17,784.6	49,414.4
Canada (British Columbia)	5,676.4	
United States	12,108.2	
North of Bristol Bay	2.8	
Bristol Bay[2]	5,715.0	
Alaska Peninsula[3]	1,625.5	
Cook Inlet	1,465.7	
Copper River area[4]	832.2	
Southeastern Alaska[5]	952.1	
Washington and Oregon[6]	1,514.9	

[1] Japan has no stocks of sockeye salmon.
[2] Includes north side of Alaska Peninsula.
[3] Includes Aleutian Islands, south side of Alaska Peninsula, Chignik, and Kodiak Island.
[4] Includes Resurrection Bay, Prince William Sound, Copper and Bering Rivers.
[5] Includes Yakutat.
[6] Includes the Columbia River (32.2 thousand fish).
Source of data: International North Pacific Fisheries Commission, 1966, 1967, and 1968; and supplemental catch statistics supplied to the INPFC by the USSR.

and North America from International North Pacific Fisheries Commission (INPFC) sources. The approximate ranking on each continent of the importance of the coastal areas is as follows:

Asia (from Hanamura, 1966 and Krogius, 1958)		*North America (from catch data of Table 1)*	
Ozernaya River	1	Bristol Bay	1
Kamchatka River	2	British Columbia	2
Bolshaya River	3	Alaska Peninsula	3
Paratunka River	4	Washington and Oregon	4
Apuka River	5	Cook Inlet	5
Okhota and Kukhtuy Rivers	6	Southeastern Alaska	6
		Copper River area	7
		Columbia River	8
		North of Bristol Bay	9

The abundance and catch of sockeye salmon in most areas can fluctuate widely between years, however. Some of these variations in catch are revealed in Appendix Table 1 of the catch of the 5 years, 1964-68, which series includes one high production year in Bristol Bay—1965.

The distribution of spawning streams in Asia extends from approximately lat 66° N near the Anadyr River southward to the tip of the Kamchatka Peninsula and the Kurile Islands, and westward to the Okhota and Kukhtuy Rivers on the northern coast of the Okhotsk Sea (Hanamura, 1966, 1967). Berg (1948) indicated that the species was very rare in northern Hokkaido Island. Krogius and Krokhin (1956) concluded that approximately 90% of the total sockeye catch along the Far Eastern Coast of the USSR was produced in the Ozernaya and Kamchatka Rivers of the Kamchatka Peninsula.

The distribution of North American spawning streams extends from the Noatak River of Kotzebue Sound in Northern Alaska, southward to the Columbia River of Oregon and Washington (Aro and Shepard, 1967; Atkinson et al., 1967). The streams can be conveniently grouped into three major geographical areas for study: (1) the Columbia River to and including British Columbia: (2) Bristol Bay, Alaska, and areas north of Bristol Bay; and (3) the area between Bristol Bay and British Columbia. In many years each area contributes about one-third of the North American catch. Normally, the catch of sockeye salmon north of Bristol Bay is insignificant in relation to the number of fish taken in the Bay, but consumption and barter of salmon is substantial, especially by residents along the Kuskokwim River.

Thus, plates of representative scales of fish from southern Kamchatka, Bristol Bay, and the areas north of Bristol Bay, central and southeastern Alaska, British Columbia, and the Columbia River (the coastal areas listed in Table 1) are included in the first part of this paper.

The scale samples used in a previous study (Mosher, 1968) with a few samples, which have recently become available from additional areas, were used for this study.[4] The areas from which these samples were collected are listed in Table 2. Figure 2 shows the approximate location of the areas mentioned in the text and on the plates.

SELECTION OF SCALE FEATURES LINKED TO VARIOUS STOCKS OR AREAS

My previous paper (Mosher, 1968) shows in detail the features of sockeye salmon scales and the range of variations in many characters. This paper continues the study of sockeye salmon scales to show the relation of many of the variations to locality and how these variations in scale characters can be used to identify the mainland origin of sockeye salmon taken in offshore waters.

A number of age groups have been found in all populations of sockeye salmon that have been studied. These age groups are based on the number of years the fish lived in fresh water and in the ocean. Over the geographical range of the species, individuals with scales showing freshwater ages from 0. to 4., ocean ages from .1 to .4, and total ages of 0.1 to

[4] Contributions of the following agencies to the salmon scale sampling program are gratefully acknowledged: The Alaska Department of Fish and Game, Juneau, Alaska; the Fisheries Research Board of Canada, Nanaimo, B.C.; the Fisheries Agency of Japan, Tokyo, Japan; and the Fish Commission of Oregon, Portland, Oreg. In addition, special thanks are given to Dr. I. Lagunov of the Pacific Institute of Fisheries Research and Oceanography (TINRO), Petropavlovsk, Kamchatka, USSR, who kindly supplied a series of samples from USSR streams.

TABLE 2.—Geographical areas where scales were taken from sockeye salmon. (Scales are available at the National Marine Fisheries Service, Northwest Fisheries Center, Seattle, Wash.)

Asia
- 1. Kamchatka River
- 2. Paratunka River
  - A. Dalnee Lake
  - B. Blizhnee Lake
- 3. Bolshaya River
- 4. Ozernaya River
- 5. Okhtosk Sea
- 6. North Pacific Ocean and Bering Sea from areas near the Kamchatka Peninsula

North America
- 7. Nome area
  - A. Salmon Lake
  - B. Unalakleet River
- 8. Kuskokwim River
- 9. Bristol Bay
  - A. Togiak River
  - B. Nushagak-Wood River System[1]
  - C. Kvichak River[1]
  - D. Naknek River[1]
    - (1) Brooks Lake
    - (2) Branch River
  - E. Egegik River[1]
  - F. Ugashik River[1]
  - G. Bear River
- 10. Aleutian Islands
  - A. Attu
  - B. Adak
  - C. Unalaska
- 11. Alaska Peninsula area[2]
  - A. King Cove
  - B. Chignik
  - C. Kodiak Island
    - (1) Karluk
    - (2) Red River
    - (3) Frazer River
- 12. Cook Inlet area[2]
  - A. Cook Inlet Fishery
  - B. Kenai River
  - C. Susitna River
    - (1) Fish Creek
    - (2) Judd Lake
    - (3) Alexander Creek
  - D. Kasilof River
  - E. Fish Creek, Knik Arm, Kenai Peninsula
  - F. Skilak Lake
  - G. Tustamina Lake (Bear Creek)
  - H. Upper Russian Lake
- 13. Copper River[2]
  - A. Haley Creek
- 14. Yakutat
  - A. Situk River
- 15. Petersburg area[2]
  - A. Kasheets
  - B. Stikine River
  - C. Salmon Bay
  - D. Tahlton Lake
  - E. Red Bay
  - F. Port Houghton
- 16. Ketchikan area[2]
  - A. Portland Canal
  - B. Moira Sound
    - (1) North Arm
    - (2) Kegan Creek
  - C. Karta Bay
  - D. Dolomi Lake and Stream
  - E. Hugh Smith Stream
  - F. Clarence Strait
  - G. Eek Bay
  - H. Hetta Bay
  - I. Nicholas Bay
  - J. Nichols Bay
  - K. Klawock Creek
  - L. Klakas Lake
  - M. Deweyville
- 17. British Columbia
  - A. Nass River
  - B. Skeena River
  - C. Rivers Inlet
  - D. Smith Inlet
  - E. Alert Bay
  - F. Nimpkish River
  - G. Fraser River
- 18. Columbia River
  - A. Main stem
  - B. Wenatchee River
  - C. Okanogan River

[1] Samples from the five major Bristol Bay rivers were taken each year since 1954. There are samples for most other areas for a number of years, but there is only one sample for some of the less important areas.
[2] Additional samples were taken, but numbers of scales were small.

[5]3.4 occur, but in most localities most fish are in age groups 1.2, 1.3, 2.2, and 2.3.

The number of years spent in fresh water varies within and between many spawning areas and influences many of the scale characters (Mosher, 1963, 1968). Only a few adult fish of age 0. or 4. are found, some fish of age 3. are found in a few areas, but fish of age 1. and 2. are present in substantial numbers in most areas. Table 3 shows the percentage freshwater age composition of sockeye salmon in stream samples (except as noted) from areas around the North Pacific Ocean available at the NMFS Northwest Fisheries Center.

Many features of sockeye salmon scales can be used in racial studies. Scientists at the NMFS Northwest Fisheries Center in Seattle have examined about 50 different features such as counts of circuli, measurement of zones and portions of zones, and various ratios based on these counts and measurements; but only scale characteristics with the greatest difference between Kamchatkan and Bristol Bay stocks have been described in our publications (Mosher et al., 1961; Mosher, 1963, 1968; Anas, 1964; Anas and Murai, 1969). In all of our studies—published and unpublished—the best features for racial studies have been in the freshwater and first ocean zones of the scale.

Because of the large number of Asian and North American spawning areas and the large number of age groups in some areas, it is evident that space is not available for examples of scales representative of each area and age group over the geographic range of the species. Scales from numerous areas are similar in many characters; consequently I will group together scales from fish of more than one stock or spawning area that have a relatively similar appearance.

The number of circuli in the freshwater and first ocean zones (counted as indicated on p. 36

[5] Age designation follows the European system, Koo (1962a): the number of winters the fish spent in fresh water since hatching, a decimal point, and the number of winters the fish spent in the ocean (see Mosher, 1968, p. 259 and 262).

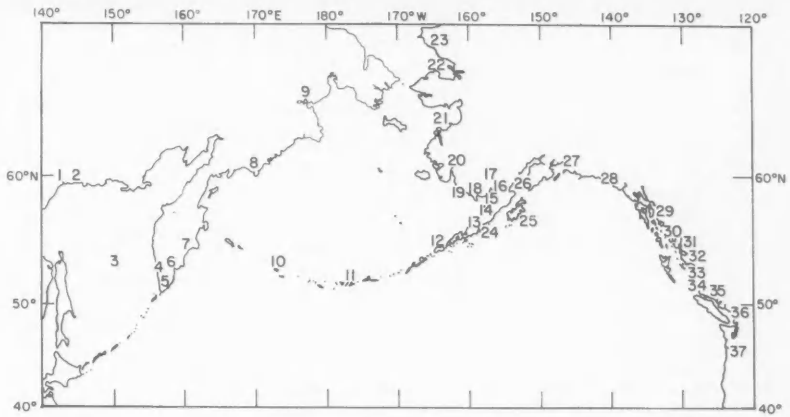

FIGURE 2.—Approximate location of areas mentioned in the text and on the plates.

1. Okhota River
2. Kukhtuy River
3. Okhotsk Sea
4. Bolshaya River
5. Ozernaya River
6. Paratunka River (Dalnee and Blizhnee Lakes)
7. Kamchatka River
8. Apuka River
9. Anadyr River
10. Attu Island
11. Adak Island
12. Unalaska Island
13. Bear and Sandy Rivers
14. Ugashik River
15. Egegik River
16. Naknek River
17. Kvichak River
18. Nushagak-Wood River system
19. Togiak Bay
20. Kuskokwim River
21. Norton Sound-Yukon River
22. Kotzebue Sound
23. Noatak River
24. Chignik Bay
25. Kodiak Island
26. Cook Inlet
27. Copper River area
28. Yakutat Bay
29. Petersburg area
30. Ketchikan area
31. Nass River
32. Skeena River
33. Rivers Inlet
34. Smith Inlet
35. Nimpkish River
36. Fraser River
37. Columbia River

and 37 of Mosher, 1963) are shown for the various areas as frequency tabulations in Tables 4 and 5 for the age 1. fish; in Tables 6 and 7 for the age 2. fish; and in Table 8 for the age 3. fish. Inspection of Tables 4 and 6 shows that the mean number of circuli in the freshwater zone varies among some geographical areas, but that in the first ocean zone (Tables 5 and 7) there is a cline in number of circuli from least in the Adak Island fish to most in the central British Columbia areas of Rivers and Smith Inlets and the Nimpkish River. A decrease in the mean number of circuli among stocks from central British Columbia southward to the Columbia River is also found. The Asian fish and those north of Bristol Bay have slightly more circuli, on the average, than those of Adak Island and Bristol Bay.

The scales from sockeye taken from certain geographic areas have similar frequency distributions of circuli in the freshwater or first ocean zone. These similarities are the basis for dividing the coast of North America into certain broad areas. When I discuss the various geographic areas, reference will be made to the appropriate frequency table.

PREPARATION OF PLATES

The scale plates for the report were made as follows: (1) The scale images produced by a scale projector like the one I described (Mosher, 1950), at 82× magnification, were photographed with a 35-mm single lens reflex camera on medium speed, fine grained film and processed to accentuate the contrast by minimum exposure

TABLE 3.—Percentage freshwater age composition of samples of sockeye salmon from geographical areas of the North Pacific Ocean from those listed in Table 2.

Locality	Year[1]	Freshwater age					Number in sample
		0.	1.	2.	3.	4.	
		— — — — — — — — *Percent* — — — — — — — —					
Asia[2]							
Ozernaya R.	1959	--	0.8	53.3	45.1	0.8	124
Bolshaya R.	1964	1.2	94.1	3.5	1.2	--	84
Kamchatka R.	1964	2.2	90.2	6.5	1.1	--	92
Paratunka R.:							
Dalnee Lake	1964	--	2.9	44.3	52.8	--	70
Blizhnee Lake	1958	--	0.6	78.5	20.3	0.6	172
Okhotsk Sea	1957	--	51.5	42.1	6.4	--	501
Off S.E. Kamchatka	1965	--	21.9	59.2	16.9	2.0	201
North America:							
Kuskokwim	1959	--	70.5	28.7	0.8	--	122
Bristol Bay:							
Ugashik R.	1966	--	39.6	60.4	--	--	318
Egegik R.	1966	--	5.9	86.9	7.2	--	305
Naknek R.	1966	--	32.0	67.2	0.8	--	356
Kvichak R.	1966	--	4.0	95.7	0.3	--	351
Nushagak R.	1966	--	94.7	5.3	--	--	322
Togiak R.	1955	3.3	80.1	16.6	--	--	307
Bear R.	1959	--	1.6	95.0	3.4	--	119
Aleutian Islands:							
Attu Isl.	1956	1.3	38.8	52.9	6.6	0.4	227
Adak Isl.	1956	--	30.6	60.5	8.0	0.9	213
Unalaska Isl.	1956	--	38.9	37.5	22.9	0.7	144
Alaska Peninsula:							
King Cove	1957	--	45.7	52.7	1.6	--	182
Chignik R.	1957	--	40.0	59.3	1.7	--	175
Karluk R.	1959	--	--	48.1	47.2	4.7	106
Red River	1959	--	--	85.1	14.9	--	107
Cook Inlet	1959	--	83.9	16.1	--	--	118
Cook Inlet Fish Cr.	1959	--	98.3	1.7	--	--	120
Southeastern Alaska:							
Copper R.	1959	--	87.7	12.3	--	--	122
Yakutat R.	1958	--	31.5	65.6	2.9	--	105
Petersburg	1964	4.6	81.8	13.0	0.6	--	323
Ketchikan	1964	0.3	84.1	15.6	--	--	352
British Columbia:							
Nass R.	1964	--	35.0	65.0	--	--	320
Skeena R.	1964	--	98.7	1.3	--	--	297
Rivers Inlet	1961	--	98.0	2.0	--	--	248
Smith Inlet	1961	--	100.0	--	--	--	255
Nimpkish R.	1967	--	64.5	30.4	5.1	--	79
Fraser R.	1964	0.7	98.0	1.3	--	--	153
Columbia River	1964	0.2	88.1	11.7	--	--	416

[1] The year selected is the most complete for that area, is in a series with adjacent areas, or is the only year a sample is available in our series (Table 2).
[2] Historical data on age composition of samples from Ozernaya, Bolshaya, and Kamchatka Rivers, and Lake Dalnee for a number of years from 1931 to 1960 are available in Hanamura (1966).

and maximum development (Adams, 1952; Mortensen, 1947). (2) Positive prints of sections that showed the important features of the anterior field of the scales were made from these negatives on high contrast enlarging paper. (3) The positive prints of the scale sections were assembled by area groups on mounting sheets and photographed to provide the plates. The scales were all photographed at the same magnification. Consequently, the relative size of the scale features on the plates reflects the relative size of the scale features themselves.

As indicated in my previous paper (Mosher, 1968), the texture, contrast, and distinctness of circuli vary greatly both on individual scales and between the scales of the same and different fish. Some scales can be photographed to show the features clearly; other scales, especially from some localities with many closely spaced and broken circuli, do not provide clear photographs of all features.

TABLE 4.—Percentage frequency distribution[1] of circuli in the total freshwater zone from age 1. sockeye salmon collected in various years from 1956 to 1967.

Number of circuli	Asia			Alaska													British Columbia						
	Kamchatka River[2]	Bolshaya River[2]	Dalnee Lake[3]	Far North[4]	Bristol Bay[5]	Attu Island[6]	Adak Island[6]	Unalaska Island[6]	Chignik[7]	Cook Inlet[8]	Fish Creek[7]	Copper River[9]	Yakutat[5]	Petersburg[2]	Ketchikan[2]	Nass River[8]	Skeena River[8]	Rivers Inlet[9]	Smith Inlet[9]	Nimpkish River[10]	Fraser River[9]	Columbia River[7]
	Percent																					
5	1.9	1.4	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0.5	--	--	--	--
6	5.6	6.5	--	--	--	--	--	--	--	--	--	1.1	--	2.2	0.5	--	--	1.9	1.0	--	--	--
7	7.4	12.0	--	--	--	0.7	--	--	--	0.5	--	3.8	0.5	6.5	1.5	--	--	4.8	4.5	--	--	--
8	9.6	14.7	--	0.4	--	2.8	--	--	--	1.5	--	4.7	3.1	11.2	2.5	--	--	10.5	8.5	0.5	--	--
9	13.3	16.4*	--	0.9	--	7.0	--	--	0.6	2.0	--	4.9	6.6	15.9*	2.5	0.5	--	18.3	12.5	0.9	--	--
10	16.7	14.0	--	1.3	--	13.0	--	--	2.8	2.0	--	6.7	9.2	15.9*	2.5	3.0	0.5	23.3*	20.0	3.9	--	--
1	18.2*	9.9	--	3.0	--	16.9*	--	--	6.0	4.0	--	9.6	11.2	12.5	7.0	5.5	2.5	20.0	23.5*	9.3	--	--
2	13.9	8.6	--	4.3	0.1	14.8*	--	--	8.5	10.5	--	14.2	12.8	10.8	14.5	4.5	6.5	11.7	15.5	9.8	0.6	0.3
3	7.4	6.2	--	3.0	1.9	9.5	--	--	12.5	18.5	--	16.9*	14.8	8.6	21.0	5.5	10.0	6.0	6.0	6.4	1.7	0.6
4	3.1	3.1	0.5	0.9	6.5	7.0	--	--	17.0*	20.5*	--	16.3	18.4*	6.5	22.5*	13.0	13.5	2.6	3.5	5.4	2.8	0.3
5	1.2	1.7	2.7	2.2	11.3	7.0	--	0.5	16.2	16.0	--	12.2	15.8	5.2	15.0	21.0*	21.0	0.5	3.5	4.9	5.6	0.6
6	1.2	1.4	5.5	7.8	15.1	5.6	--	3.7	11.1	11.5	--	5.8	6.1	3.0	6.0	21.0*	23.5*	--	1.5	3.4	10.1	1.8
7	0.6	1.4	5.5	12.4	18.6	3.5	0.8	7.9	8.0	7.5	--	2.3	1.0	1.3	2.0	13.5	15.0	--	--	4.9	14.6	2.1
8	--	1.0	7.3	19.8	19.5*	3.2	4.0	7.9	7.1	3.5	--	1.1	0.5	0.4	1.0	7.0	6.0	--	--	10.3	16.6*	4.3
9	--	0.7	14.1	22.8*	15.5	3.2	8.5	6.5	5.4	1.5	0.3	0.3	--	--	1.0	3.5	1.5	--	--	13.7*	13.5	10.1
20	--	0.7	17.7*	13.8	8.7	2.1	10.9	6.5	2.6	0.5	0.9	--	--	--	0.5	1.5	--	--	--	9.8	10.4	14.3
1	--	0.3	15.5	5.2	2.6	0.7	11.3	5.6	1.1	--	5.2	--	--	--	--	0.5	--	--	--	5.4	10.1	16.8
2	--	--	14.1	1.7	0.1	0.4	11.3	4.2	0.9	--	14.3	--	--	--	--	--	--	--	--	4.4	8.4	17.1*
3	--	--	11.4	--	--	0.7	11.7	5.1	0.3	--	21.0	--	--	--	--	--	--	--	--	2.5	4.5	14.3
4	--	--	4.1	--	--	0.7	12.5*	9.2	--	--	22.6*	--	--	--	--	--	--	--	--	0.9	1.1	10.7
5	--	--	0.5	--	--	0.7	10.5	13.0*	--	--	18.9	--	--	--	--	--	--	--	--	0.9	--	5.2
6	--	--	0.9	--	--	0.4	6.0	11.1	--	--	11.0	--	--	--	--	--	--	--	--	0.5	--	1.2
7	--	--	0.5	--	--	--	3.6	6.9	--	--	4.6	--	--	--	--	--	--	--	--	0.5	--	0.3
8	--	--	--	--	--	--	3.6	5.6	--	--	1.2	--	--	--	--	--	--	--	--	0.9	--	--
9	--	--	--	--	--	--	3.6	4.2	--	--	--	--	--	--	--	--	--	--	--	0.5	--	--
30	--	--	--	--	--	--	1.6	1.9	--	--	--	--	--	--	--	--	--	--	--	--	--	--
1	--	--	--	--	--	--	--	0.5	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Number of fish	81	73	55	58	181	71	62	54	88	50	82	86	49	58	50	50	50	105	50	51	89	82

[1] Actual frequencies smoothed according to Henry (1961).
[2] 1964.
[3] 1958.
[4] 1957.
[5] 1966.
[6] 1956.
[7] 1963.
[8] 1965.
[9] 1961.
[10] 1967.
* Indicates modes.

TABLE 5.—Percentage frequency distribution[1] of circuli in the first ocean zone of age 1. sockeye salmon collected in various years from 1956 to 1967.

Number of circuli	Asia			Alaska												British Columbia						
	Kamchatka River[2]	Bolshaya River[2]	Dalnee Lake[3]	Far North[4]	Bristol Bay[5]	Attu Island[6]	Adak Island[6]	Unalaska Island[6]	Chignik[7]	Cook Inlet[8]	Fish Creek[7]	Copper River[9]	Yakutat[5]	Petersburg[2]	Ketchikan[2]	Nass River[3]	Skeena River[8]	Rivers Inlet[9]	Smith Inlet[9]	Nimpkish River[10]	Fraser River[9]	Columbia River[7]
												Percent										
10	--	--	--	--	--	--	0.1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
11	--	--	--	--	--	--	0.9	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
2	--	--	--	--	--	--	2.7	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
3	--	--	--	--	0.1	0.1	5.9	0.2	--	--	--	--	--	--	--	--	--	--	--	--	--	--
4	--	--	--	--	0.4	0.4	10.0	1.2	--	--	--	--	--	--	--	--	--	--	--	--	--	--
5	--	--	--	--	1.1	0.8	12.6	3.4	--	--	--	--	--	--	--	--	--	--	--	--	--	--
6	--	--	--	0.4	3.9	1.2	13.3*	5.4	--	--	--	--	--	--	--	--	--	--	--	--	--	--
7	--	0.3	1.4	2.2	8.6	2.6	13.2*	7.0	--	--	--	--	--	--	--	--	--	--	--	--	--	--
8	1.2	0.7	3.2	5.2	12.3	5.1	10.8	9.6	0.6	--	--	--	--	--	--	--	--	--	--	--	--	--
9	3.1	0.7	3.6	9.1	16.7	7.3	8.4	13.7	1.4	2.0	0.9	--	--	--	--	--	--	--	--	--	--	--
20	3.7	1.0	5.9	11.2	21.0*	12.6	7.4	14.8*	2.3	6.5	2.7	0.3	--	--	--	--	--	--	--	--	0.3	--
1	6.8	4.5	12.3	15.5	18.1	16.9*	5.8	11.2	4.5	11.0	5.5	0.9	--	1.3	--	0.5	--	--	--	--	0.6	0.9
2	12.3	12.3	19.1	21.1*	10.5	14.9	3.8	9.5	8.5	13.5	11.0	2.0	--	3.0	0.5	1.5	0.5	--	--	--	1.4	4.0
3	17.6	19.5	20.0*	17.2	5.0	13.2	2.3	8.9	14.2	17.0	17.4	4.1	1.0	2.5	2.0	3.0	3.0	--	--	--	5.1	7.3
4	20.7*	21.2*	15.5	10.3	1.9	11.5	1.5	6.4	17.3*	20.0*	18.9*	6.4	4.1	2.2	3.0	4.5	10.5	--	--	--	9.8	9.8
5	17.2	18.1	10.5	6.0	0.4	6.7	0.7	3.9	15.6	14.5	16.2	9.9	12.2	6.0	5.5	6.5	16.0	0.5	0.5	--	12.6	14.0
6	10.5	12.0	5.9	1.7	--	2.7	0.2	2.0	13.4	7.5	13.4	14.5	23.0*	13.4	13.0	11.5	13.5	1.4	1.5	--	13.5*	18.0*
7	4.9	5.8	2.3	--	--	1.4	0.2	1.2	9.9	5.0	8.8	16.3*	23.0*	17.7*	18.0*	15.5*	13.5	1.7	4.0	1.5	12.4	16.8
8	1.5	2.7	0.5	--	--	1.3	0.1	1.1	6.0	2.5	3.3	14.8	14.8	16.4	16.0	14.0	16.5*	1.4	6.5	3.9	11.5	12.2
9	0.3	1.0	--	--	--	0.9	--	0.4	3.7	0.5	0.9	11.9	11.2	13.8	13.5	9.5	14.0	2.9	8.0	7.4	11.5	8.2
30	--	--	--	--	--	0.3	--	--	2.0	--	0.6	7.0	8.2	10.8	11.5	7.5	7.0	6.2	9.0	11.8	9.3	5.2
1	--	--	--	--	--	--	--	--	0.6	--	0.3	4.1	2.6	5.6	7.5	10.0*	2.5	8.8	7.5	11.8	6.2	2.4
2	--	--	--	--	--	--	--	--	--	--	--	3.2	--	2.2	4.5	10.0*	2.0	11.2	7.0	10.8	3.9	0.9
3	--	--	--	--	--	--	--	--	--	--	--	1.7	--	1.7	3.5	5.0	1.0	13.8	8.0	13.7	1.7	0.3
4	--	--	--	--	--	--	--	--	--	--	--	1.5	--	1.7	1.5	1.0	--	14.0*	8.5	14.7*	0.3	--
5	--	--	--	--	--	--	--	--	--	--	--	1.1	--	1.3	--	--	--	12.1	10.5	11.8	--	--
6	--	--	--	--	--	--	--	--	--	--	--	0.3	--	0.4	--	--	--	8.8	12.5*	7.4	--	--
7	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	6.2	10.0	3.4	--	--
8	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	4.8	4.5	1.5	--	--
9	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2.9	1.5	0.5	--	--
40	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1.9	0.5	--	--	--
1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1.2	--	--	--	--
2	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0.2	--	--	--	--
Number of fish	81	73	55	58	181	181	203	140	88	50	82	86	49	58	50	50	50	105	50	51	89	82

[1] Actual frequencies smoothed according to Henry (1961).
[2] 1964.
[3] 1958.
[4] 1957.
[5] 1966.
[6] 1956, ages 1. and 2. combined.
[7] 1963.
[8] 1965.
[9] 1961.
[10] 1967.
* Indicates modes.

TABLE 6.—Percentage frequency distribution[1] of circuli in the total freshwater zone of age 2. sockeye salmon collected in various years from 1956 to 1967.

Number of circuli	Asia			Alaska										British Columbia	
	Ozernaya River[2]	Blizhnee Lake[3]	Dalnee Lake[3]	Far North[4]	Bristol Bay[5]	Attu Island[6]	Adak Island[6]	Unalaska Island[6]	Chignik[7]	Cook Inlet[8]	Karluk River[9]	Yakutat[5]	Ketchikan[10]	Nass River[5]	Nimpkish River[11]
	Percent														
9	--	0.5	--	--	--	0.4	--	--	--	--	--	--	--	--	--
10	--	2.9	--	--	--	2.4	--	--	1.2	--	--	--	--	--	--
1	--	10.3	--	--	--	5.5	--	--	8.5	--	--	2.4	--	--	--
2	0.3	18.6	--	--	--	9.3	--	--	16.1*	--	--	6.0	--	--	--
3	0.7	20.1*	--	1.2	--	12.9	--	--	13.3	0.3	--	11.9	--	--	--
4	0.7	16.2	--	4.5	0.2	14.0*	--	--	7.7	3.0	--	20.2*	0.5	--	--
5	2.4	11.3	--	8.2	1.9	12.1	--	0.9	7.3	6.9	--	19.0	4.0	--	--
6	5.6	6.9	--	12.7	4.4	8.8	--	3.7	9.7	10.2	0.5	13.1	8.5	1.1	--
7	9.4	4.4	--	16.4*	6.8	7.9	0.2	6.9	12.5	11.8*	4.0	11.9	11.5	5.7	--
8	14.6	3.9	--	16.4*	10.0	7.4	0.4	7.9	12.1	11.5	10.0	8.3	15.5	10.2	1.0
9	16.3*	2.9	--	13.9	11.9	4.8	0.9	7.9	7.3	10.9	12.5	3.6	16.5*	13.6	3.1
20	14.6	1.5	--	9.4	13.1	3.3	2.5	10.2*	2.4	11.5	12.0	2.4	13.5	19.3*	5.2
1	13.2	0.5	--	7.0	14.8*	2.6	5.8	10.2*	0.4	11.8*	15.0	1.2	11.5	18.2	5.2
2	9.7	--	--	6.6	14.1	2.4	9.7	6.9	--	10.5	18.5*	--	9.5	10.2	3.1
3	5.9	--	--	3.3	11.3	2.6	13.1	6.9	0.4	5.9	14.5	--	5.5	8.0	2.1
4	4.2	--	--	0.4	7.4	1.4	15.5*	9.2	0.8	2.6	7.0	--	1.5	8.0	2.1
5	2.1	--	--	--	3.0	0.7	15.3	9.7	0.4	1.3	3.5	--	--	4.5	2.1
6	0.3	--	--	--	0.8	0.9	13.3	7.9	--	0.3	2.0	--	0.5	1.1	3.1
7	--	--	0.7	--	0.2	0.4	10.2	5.1	--	0.3	0.5	--	1.0	--	5.2
8	--	--	5.3	--	--	--	6.5	2.8	--	0.7	--	--	0.5	--	4.2
9	--	--	10.5	--	--	--	3.2	1.9	--	0.3	--	--	--	--	2.1
30	--	--	11.2	--	--	--	1.3	1.4	--	--	--	--	--	--	3.1
1	--	--	12.5	--	--	--	0.7	0.5	--	--	--	--	--	--	4.2
2	--	--	16.4*	--	--	--	0.5	--	--	--	--	--	--	--	7.3
3	--	--	16.4*	--	--	--	0.4	--	--	--	--	--	--	--	12.5*
4	--	--	10.5	--	--	--	0.4	--	--	--	--	--	--	--	11.5
5	--	--	5.9	--	--	--	0.2	--	--	--	--	--	--	--	6.2
6	--	--	5.3	--	--	--	--	--	--	--	--	--	--	--	4.2
7	--	--	3.9	--	--	--	--	--	--	--	--	--	--	--	5.2
8	--	--	1.3	--	--	--	--	--	--	--	--	--	--	--	5.2
9	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2.1
Number of fish	72	51	38	61	216	105	139	54	62	76	50	21	50	22	24

[1] Actual frequencies smoothed according to Henry (1961).
[2] 1959.
[3] 1958.
[4] 1957.
[5] 1966.
[6] 1956.
[7] 1961.
[8] 1963.
[9] 1965.
[10] 1964.
[11] 1967.
* Indicates modes.

DESCRIPTION OF SCALES FROM FISH OF VARIOUS AREAS

The scale photographs are shown in three major series: ages 1., 2., and 3. Representative scales from each broad coastal area with relatively similar scales (including specific scale types from some areas of small production, when necessary) are shown on one plate. Two exceptions to this grouping are made: (1) distinctive scales from age 1. fish from North American areas are shown on two plates and those for age 2. fish on one plate; and (2) scales from fish from North American areas north of Bristol Bay of ages 1., 2., and 3. are shown on the same plate. Scales of age 0. fish from all areas are shown on one plate, and those of age 4. fish from all areas are shown on another plate.

A reference to the appropriate frequency tables of the number of circuli in the freshwater and first ocean zones (Tables 4 to 8) is made for each area group. These tables should be referred to as scales from each group are discussed.

TABLE 7.—Percentage frequency distribution[1] of circuli in the first ocean zone of age 2. sockeye salmon collected in various years from 1956 to 1967.

Number of circuli	Asia			Alaska										British Columbia	
	Ozernaya River[2]	Blizhnee Lake[3]	Dalnee Lake[3]	Far North[4]	Bristol Bay[5]	Attu Island[6]	Adak Island[6]	Unalaska Island[6]	Chignik[7]	Cook Inlet[8]	Karluk River[9]	Yakutat[5]	Ketchikan[10]	Nass River[5]	Nimpkish River[11]
	Percent														
11	--	--	--	--	--	--	0.9	--	--	--	--	--	--	--	--
2	--	--	--	--	--	--	2.7	--	--	--	--	--	--	--	--
3	--	--	--	--	--	0.1	5.9	0.2	--	--	--	--	--	--	--
4	--	--	--	--	0.3	0.4	10.0	1.2	--	--	--	--	--	--	--
5	--	--	--	--	1.2	0.8	12.6	3.4	--	--	--	--	--	--	--
6	--	--	--	--	3.4	1.2	13.3*	5.4	--	--	--	--	--	--	--
7	--	--	2.0	2.0	8.0	2.6	13.2	7.0	--	--	--	--	--	--	--
8	--	--	5.3	7.0	13.1	5.1	10.8	9.6	--	--	--	--	--	--	--
9	0.3	--	7.9	9.8	17.9	7.3	8.4	13.7	--	0.7	0.5	--	--	--	--
20	1.7	1.0	13.8	12.7	20.9*	12.6	7.4	14.8*	0.4	3.0	1.5	--	--	--	--
1	3.1	5.9	21.1*	16.4*	17.8	16.9*	5.8	11.2	4.0	6.9	4.5	--	0.5	--	--
2	6.6	11.8	21.1*	15.6	10.5	14.9	3.8	9.5	8.1	9.5	7.5	--	2.0	--	--
3	16.0	13.2	13.8	13.5	4.5	13.2	2.3	8.9	8.9	10.9	8.5	2.4	3.5	--	--
4	24.0*	14.7	7.9	10.7	1.5	11.5	1.5	6.4	11.3	15.5	12.5	14.3	5.0	1.1	1.0
5	22.2	18.6*	5.3	6.6	0.5	6.7	0.7	3.9	14.5	18.4*	15.0	25.0*	10.0	3.4	3.1
6	14.2	16.7	2.0	3.7	0.2	2.7	0.2	2.0	16.1	13.8	14.5	21.4	15.0*	8.0	5.2
7	7.3	9.3	--	1.6	0.1	1.4	0.2	1.2	16.9*	9.2	16.5*	16.7	14.5	20.5	6.2
8	3.5	4.9	--	0.4	--	1.3	0.1	1.1	13.3	6.9	13.5	13.1	13.0	29.5*	8.3
9	1.0	2.5	--	--	--	0.9	--	0.4	5.6	3.3	5.0	6.0	12.5	21.6	16.7
30	--	1.0	--	--	--	0.3	--	--	0.8	1.3	0.5	1.2	10.0	9.1	22.9*
1	--	0.5	--	--	--	--	--	--	--	0.7	--	--	6.5	2.3	16.7
2	--	--	--	--	--	--	--	--	--	--	--	--	4.5	--	8.3
3	--	--	--	--	--	--	--	--	--	--	--	--	2.5	1.1	5.2
4	--	--	--	--	--	--	--	--	--	--	--	--	0.5	2.3	2.1
5	--	--	--	--	--	--	--	--	--	--	--	--	--	1.1	1.0
6	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2.1
7	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1.0
Number of fish	72	51	38	61	216	191	203	140	62	76	50	21	50	22	24

[1] Actual frequencies smoothed according to Henry (1961).
[2] 1959.
[3] 1958.
[4] 1957.
[5] 1966.
[6] 1956, ages 1 and 2 combined.
[7] 1961.
[8] 1963.
[9] 1956.
[10] 1964.
[11] 1967.
* Indicates modes.

KEY TO THE PLATES

To compensate for the reduction of the original scale photographs to fit the printed page, use a 3 to 5× reading or magnifying glass to study them.

The area enclosed by the first or central circulus is the focus or central platelet of the scale.

The long black pointers near the focus indicate winter marks in the freshwater growth zone.

A black stub pointer, if present, indicates the end of plus or transitional growth. If plus growth is present, the circuli between the outermost long black pointer and the black stub pointer are plus growth circuli. If no plus growth is present, the outermost black pointer indicates the end of freshwater growth as well as the last winter in fresh water.

The white pointers bordered by black indicate the first winter mark in the ocean growth. The circuli between the end of the freshwater growth (or plus growth, if present) and this pointer are ocean-growth circuli and record the first year's growth in the ocean (the first ocean growth zone). The more widely spread circuli of this zone were deposited from May or June to September or October (the summer growth), whereas the more closely spaced circuli near the pointer were deposited during the autumn, winter, and early spring months (the winter growth).

If a small white pointer is present, it indicates an adventitious check in the first ocean growth

TABLE 8.—Percentage frequency distribution[1] of circuli (A) in the total freshwater zone and (B) in the first ocean zone of age 3. sockeye salmon collected in various years from 1955 to 1964.

Number of circuli	(A) Asia			North America		(B) Asia			North America	
	Asia[2]	Blizhnee Lake[3]	Dalnee Lake[4]	Bristol Bay[5]	Karluk River[6]	Asia[2]	Blizhnee Lake[3]	Dalnee Lake[4]	Bristol Bay[5]	Karluk River[6]
	Percent									
12	--	0.6	--	--	--	--	--	--	--	--
3	--	4.1	--	--	--	--	--	--	--	--
4	--	9.9	--	--	--	--	--	--	0.4	--
5	0.5	15.1	--	--	--	--	--	--	1.2	--
6	2.9	19.2*	--	--	--	--	--	--	3.3	--
7	8.8	17.4	--	--	--	--	--	--	7.1	--
8	15.9	11.6	--	--	--	--	--	2.7	12.1	--
9	18.1*	9.9	--	1.0	--	1.0	--	8.1	17.9	0.3
20	16.9	8.1	--	2.0	--	2.9	--	10.1	19.6*	1.9
1	14.5	3.5	--	4.0	1.0	5.9	--	11.5	15.4	4.8
2	7.8	0.6	--	10.0	3.2	10.8	1.2	16.9	10.8	7.6
3	2.2	--	--	12.0	6.6	16.4	5.8	18.9*	6.7	13.0
4	1.2	--	--	13.0	9.5	20.1*	12.2	15.5	2.9	20.2
5	1.5	--	--	19.0*	11.4	19.1	15.1	10.8	1.7	20.9*
6	1.2	--	--	17.0	13.3	13.5	16.3	4.7	0.8	14.8
7	1.7	--	--	10.0	12.7	6.4	18.0*	0.7	--	8.6
8	2.5	--	0.7	6.0	12.1	2.2	16.3	--	--	3.8
9	2.0	--	4.1	3.0	14.2*	1.2	10.5	--	--	1.9
30	1.2	--	8.1	2.0	10.2	0.5	4.1	--	--	1.6
1	0.7	--	8.1	1.0	4.1	--	0.6	--	--	0.6
2	0.2	--	6.1	--	1.2	--	--	--	--	--
3	--	--	8.1	--	0.3	--	--	--	--	--
4	--	--	11.5*	--	--	--	--	--	--	--
5	--	--	8.1	--	--	--	--	--	--	--
6	--	--	6.8	--	--	--	--	--	--	--
7	--	--	11.5*	--	--	--	--	--	--	--
8	--	--	11.5*	--	--	--	--	--	--	--
9	--	--	8.1	--	--	--	--	--	--	--
40	--	--	4.1	--	--	--	--	--	--	--
1	--	--	0.7	--	--	--	--	--	--	--
2	--	--	--	--	--	--	--	--	--	--
3	--	--	--	--	--	--	--	--	--	--
4	--	--	--	--	--	--	--	--	--	--
5	--	--	--	--	--	--	--	--	--	--
6	--	--	0.7	--	--	--	--	--	--	--
7	--	--	1.4	--	--	--	--	--	--	--
8	--	--	0.7	--	--	--	--	--	--	--
Number of fish	102	43	37	25	79	102	43	37	25	79

[1] Actual frequencies smoothed according to Henry (1961).
[2] 1962, from an area off southeast Kamchatka.
[3] 1958.
[4] 1964.
[5] 1955 and 1957 combined.
[6] 1961.
* Indicates modes.

zone. Adventitious checks in other zones are not noted.

AGE 0., ALL AREAS (Plate 1)

As noted previously, age 0. sockeye salmon are not common anywhere since fish of this species normally live for one or more years in a lake before migrating to the sea. Consequently, it was not possible to assemble frequency distributions of the number of circuli in the first ocean zone for age 0. fish. It appears, however, that usually there are a few more circuli in the first ocean zone of scales of age 0. than on scales from fish of the same geographical area that have lived one or more years in fresh water.

A few individuals of this age have been found at some time in almost every locality. Gilbert

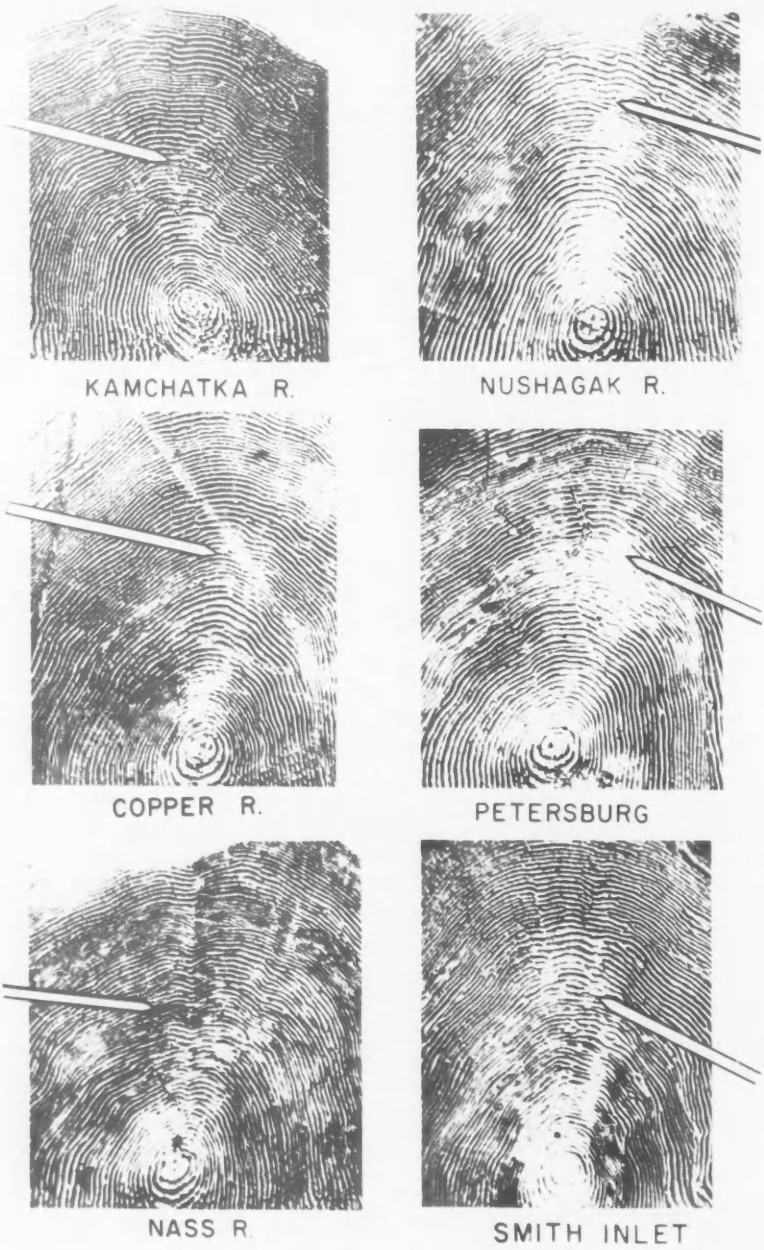

PLATE 1.—Age 0., all areas.

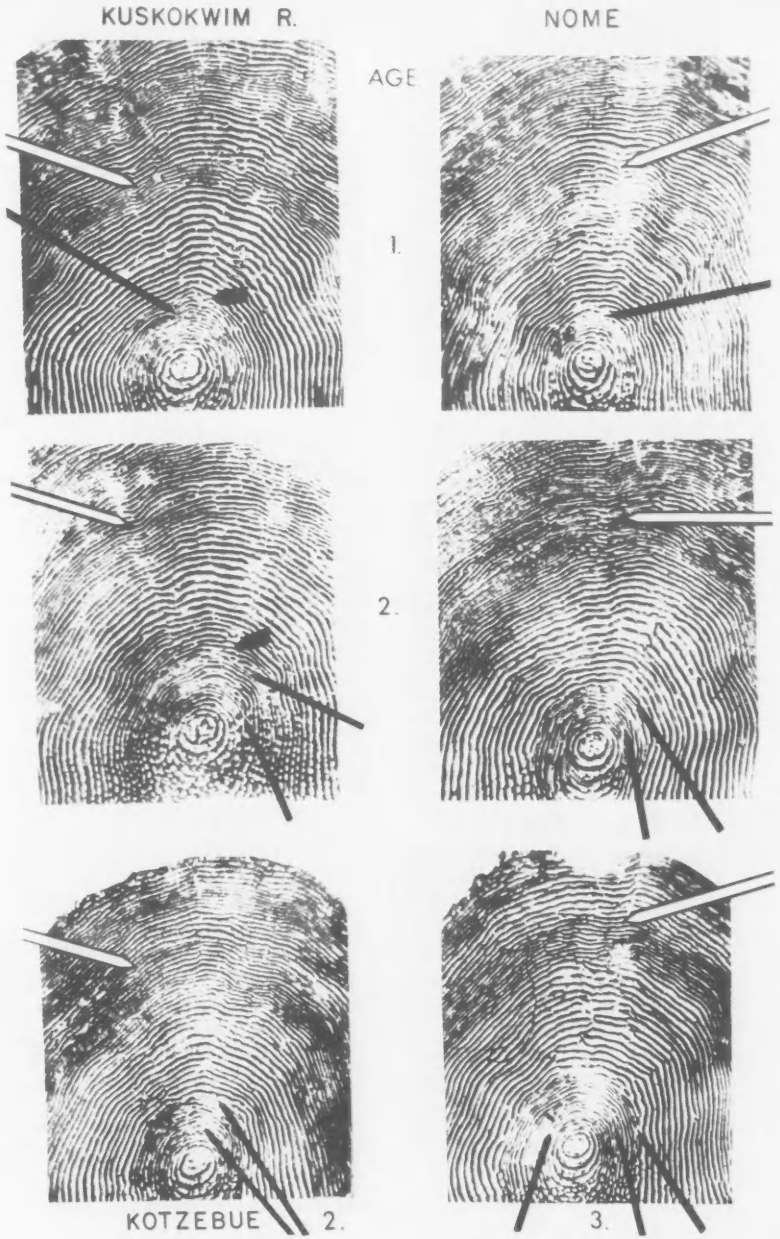

PLATE 2.—Ages 1., 2., and 3., Alaskan areas north of Bristol Bay.

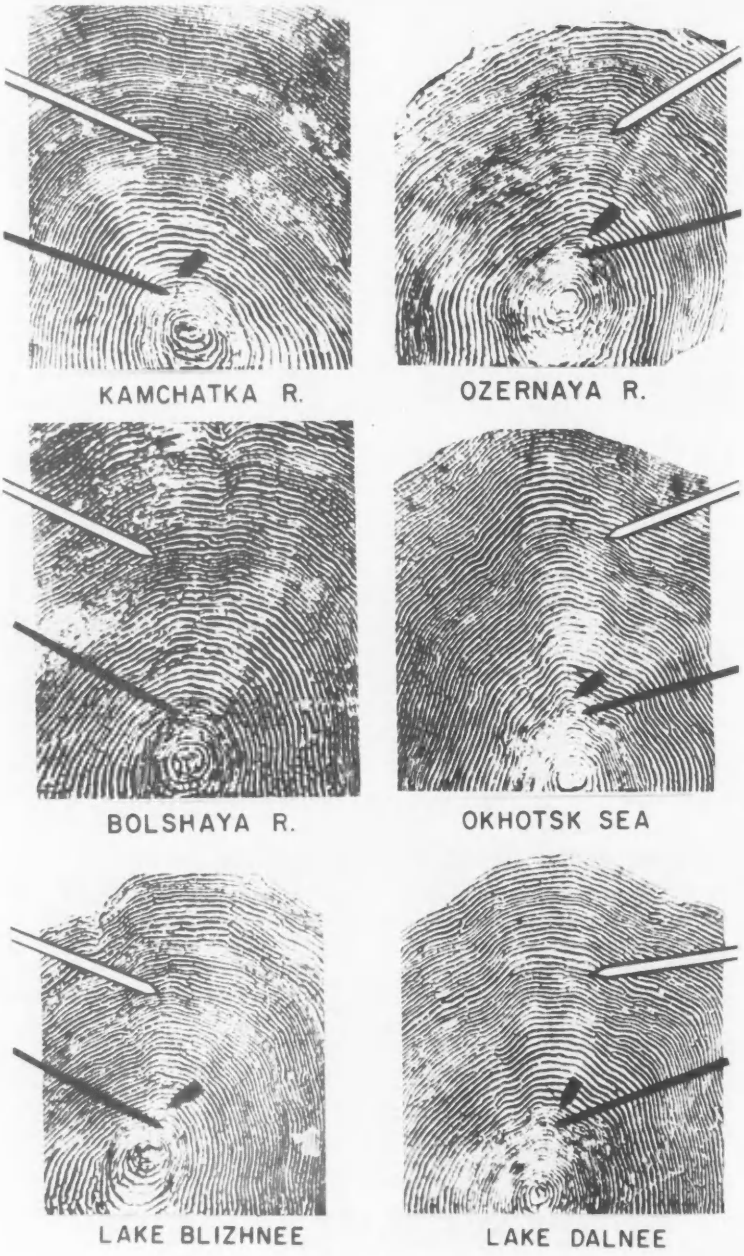

PLATE 3.—Age 1., Asia.

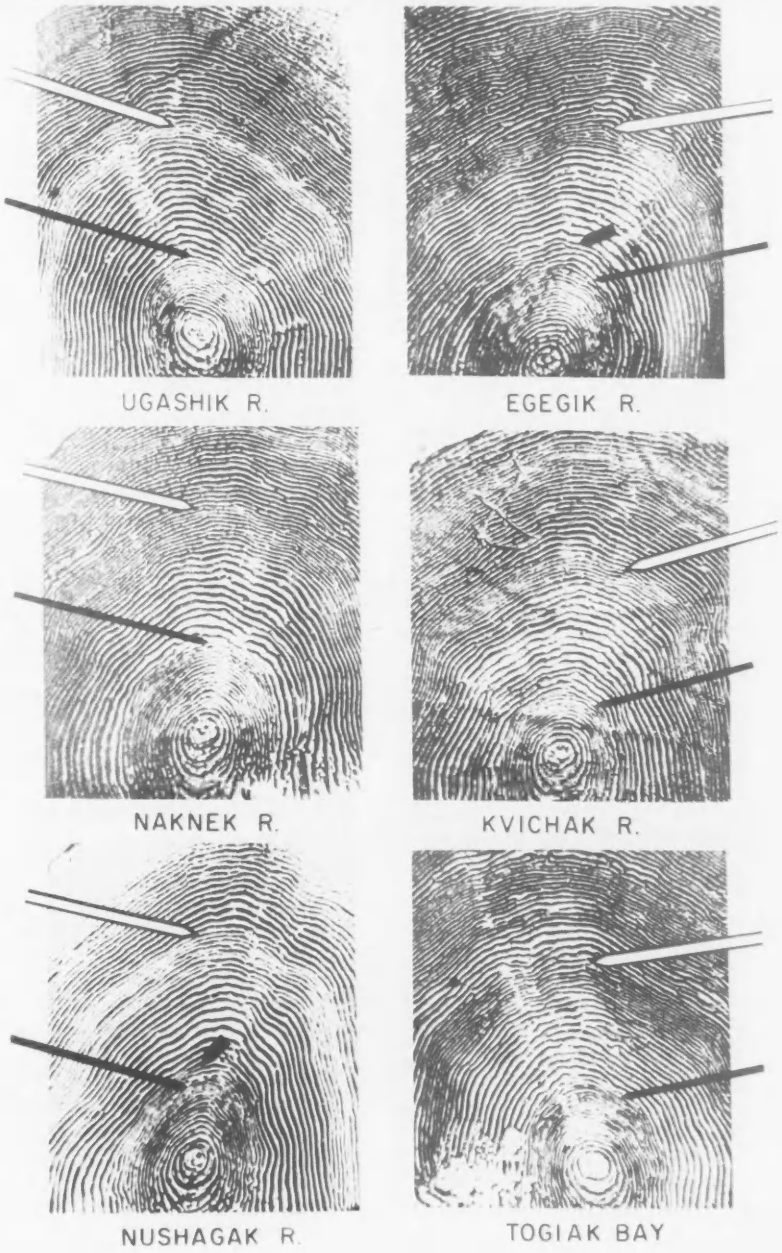

PLATE 4.—Age 1., Bristol Bay.

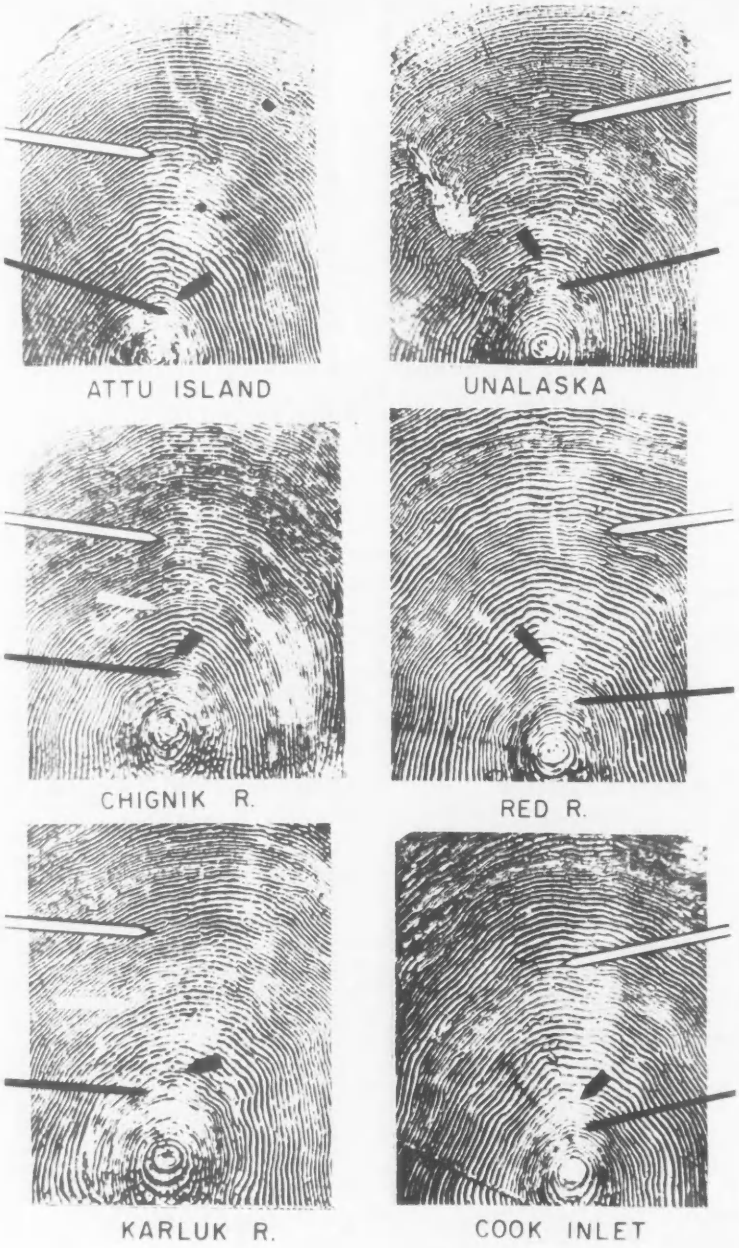

PLATE 5.—Age 1., Aleutian Islands to Cook Inlet.

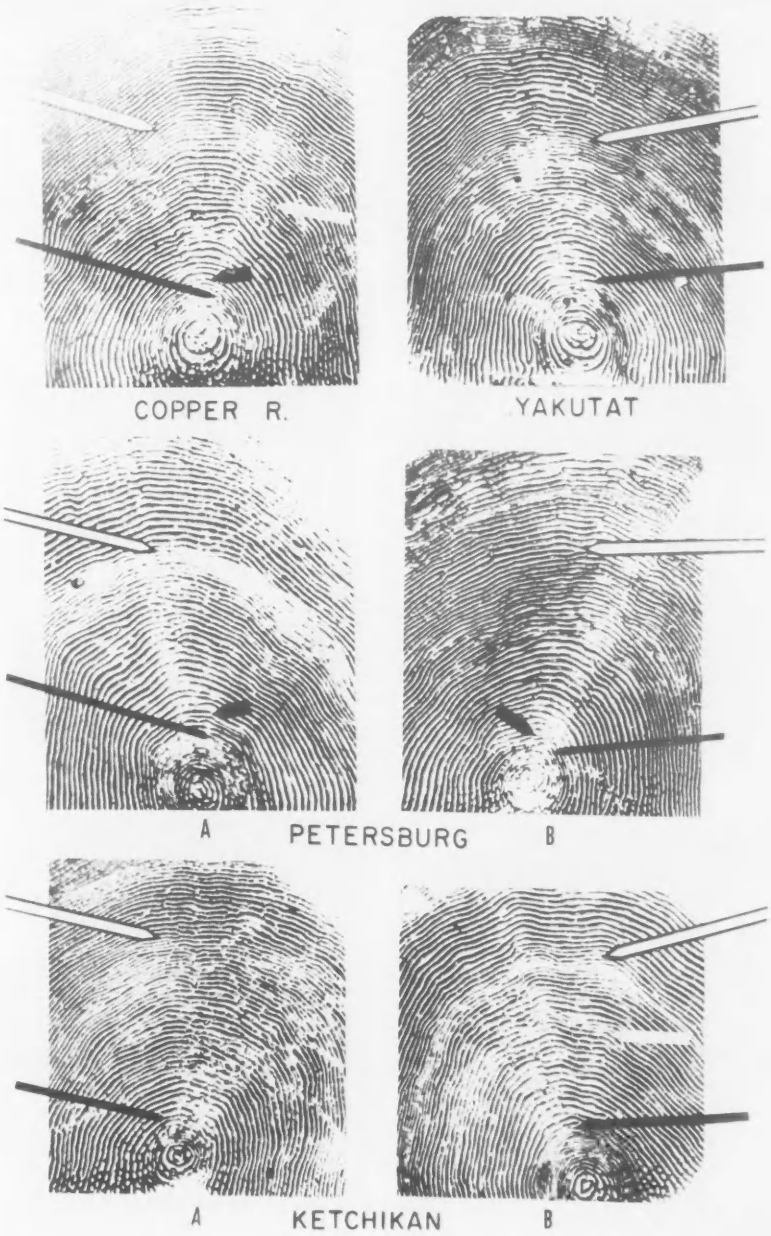

PLATE 6.—Age 1., Copper River to southeastern Alaska.

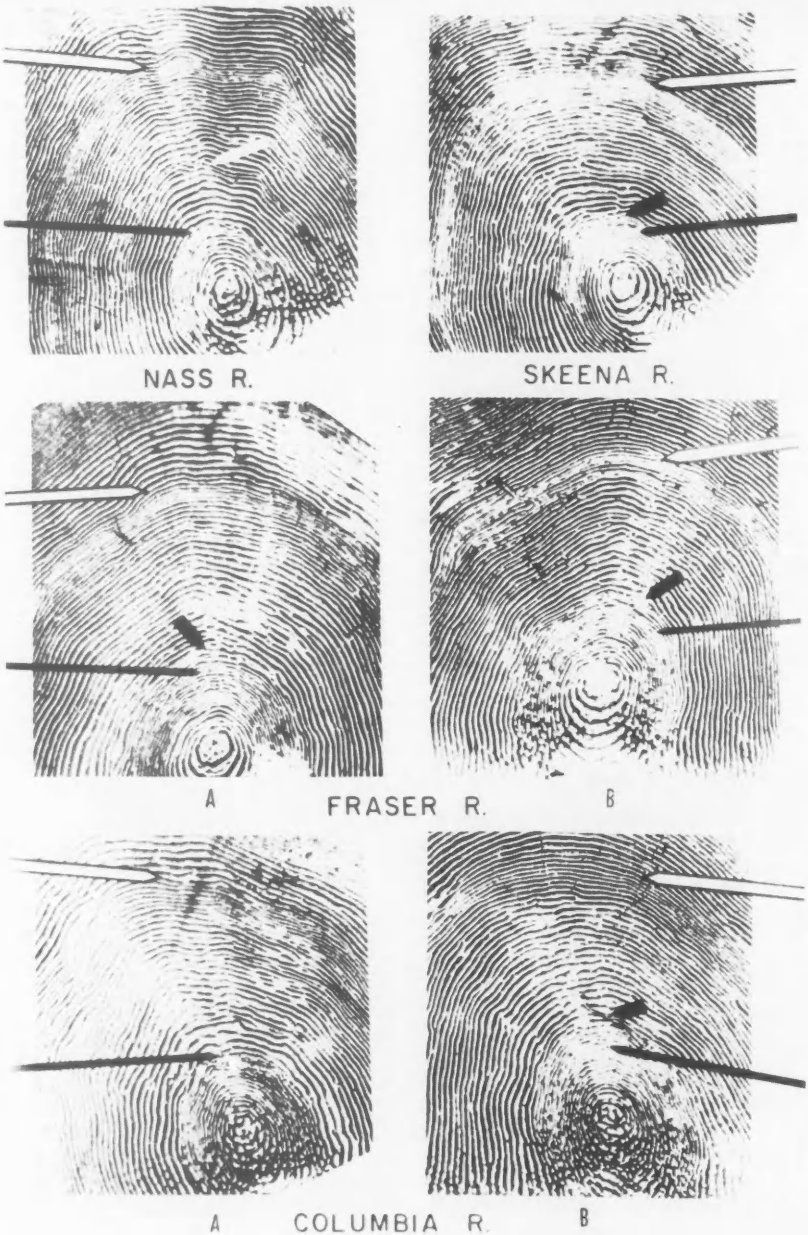

PLATE 7.—Age 1., British Columbia and the Columbia River.

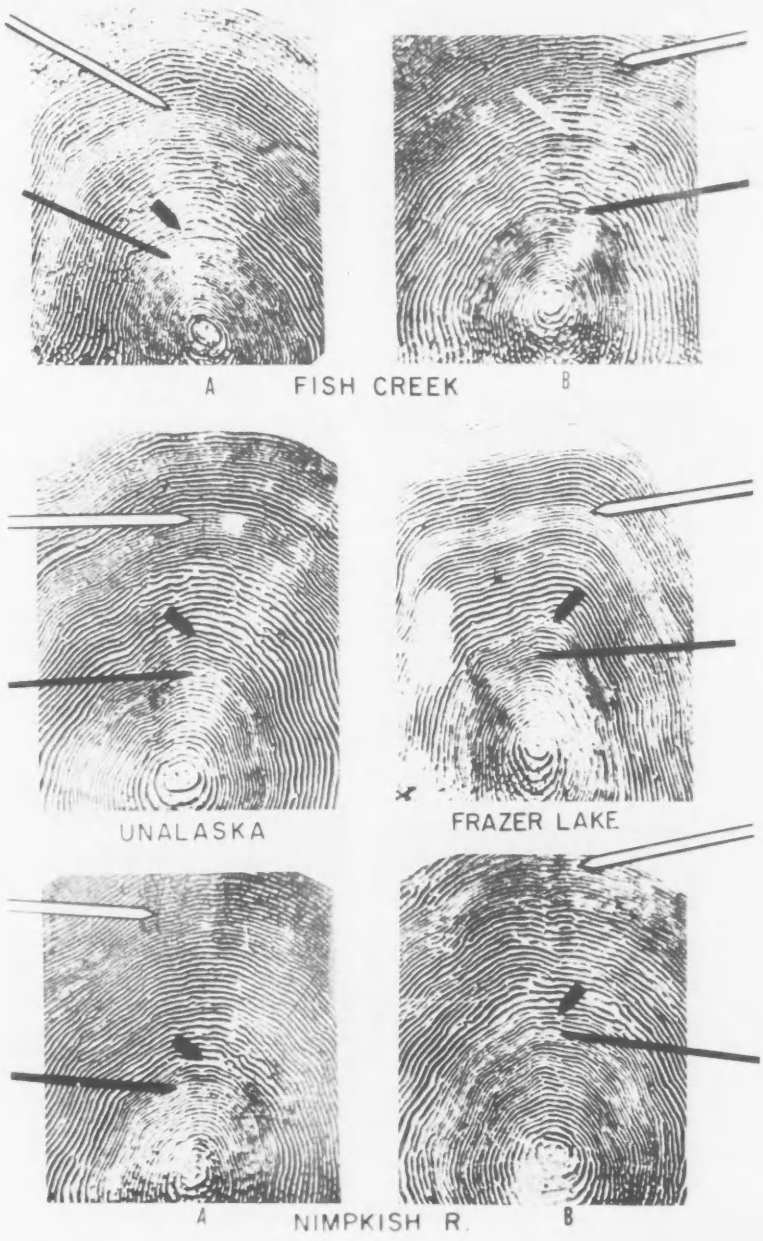

PLATE 8.—Age 1., North American areas with distinctive scales, Fish Creek type.

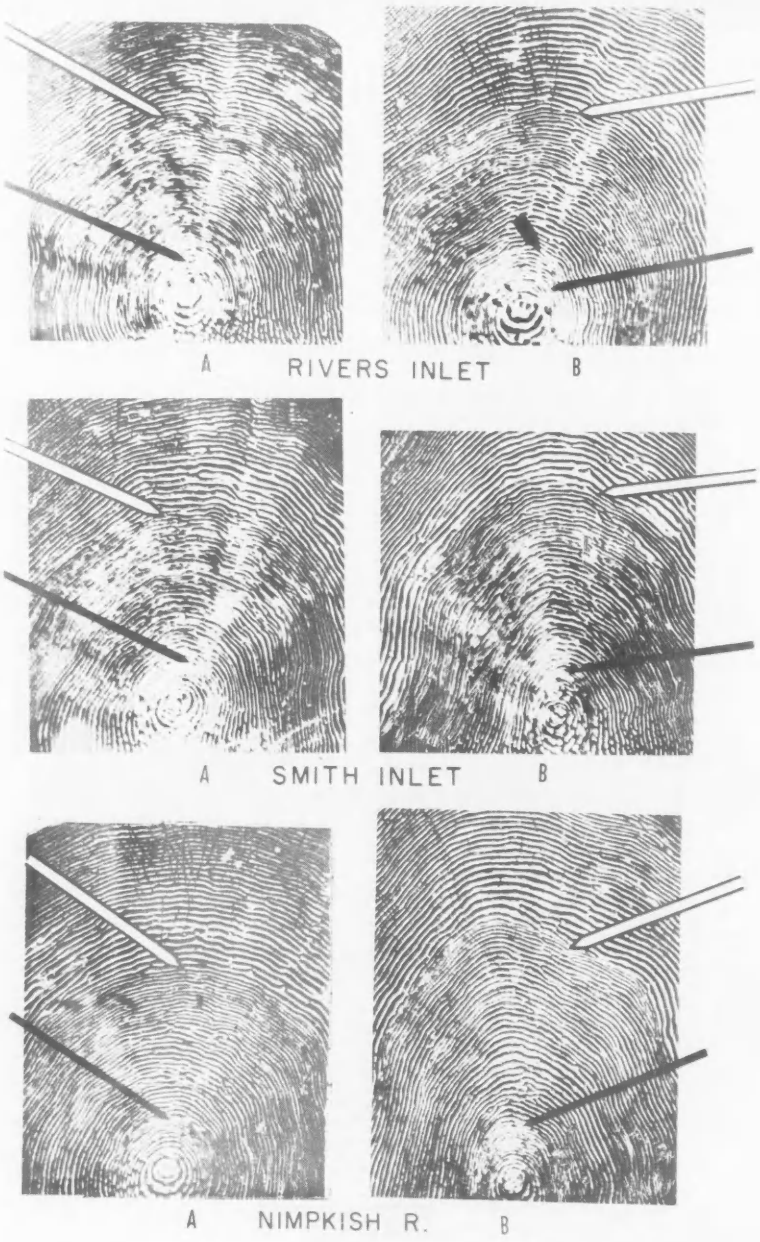

PLATE 9.—Age 1., North American areas with distinctive scales, Rivers Inlet type.

PLATE 10.—Age 2., Asia.

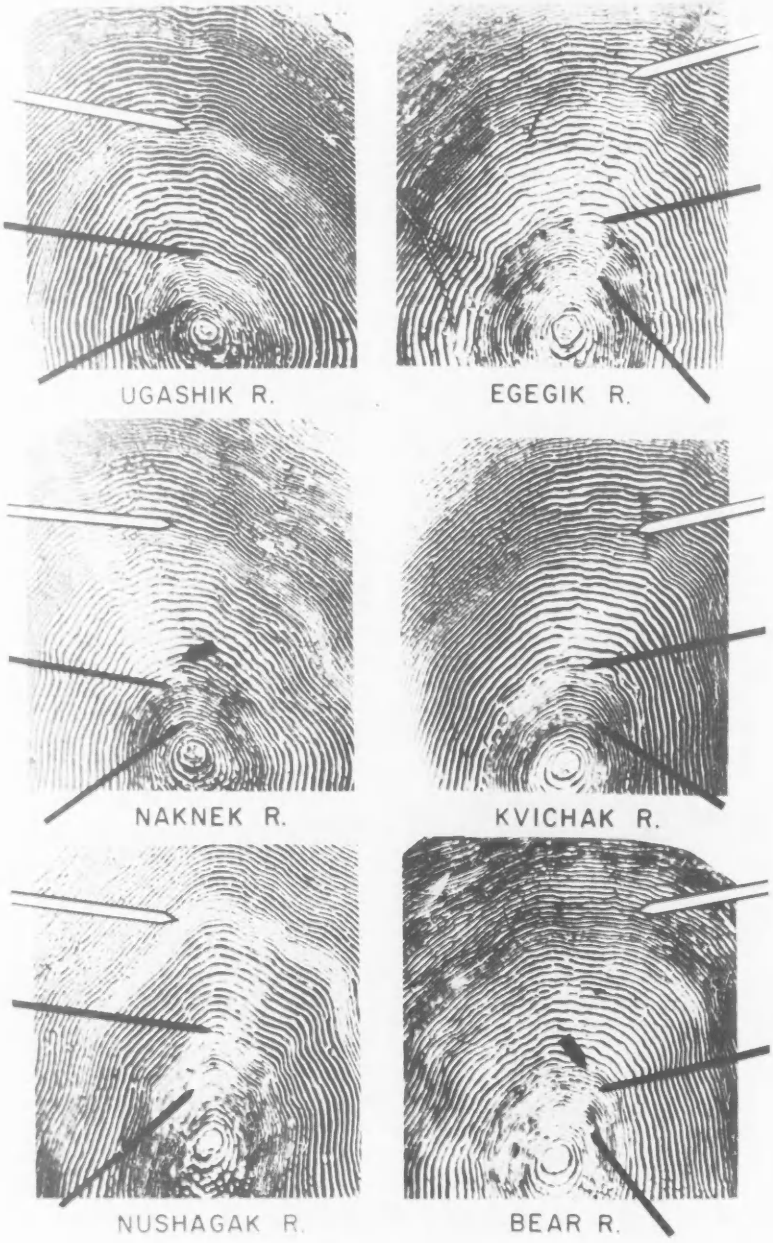

PLATE 11.—Age 2., Bristol Bay.

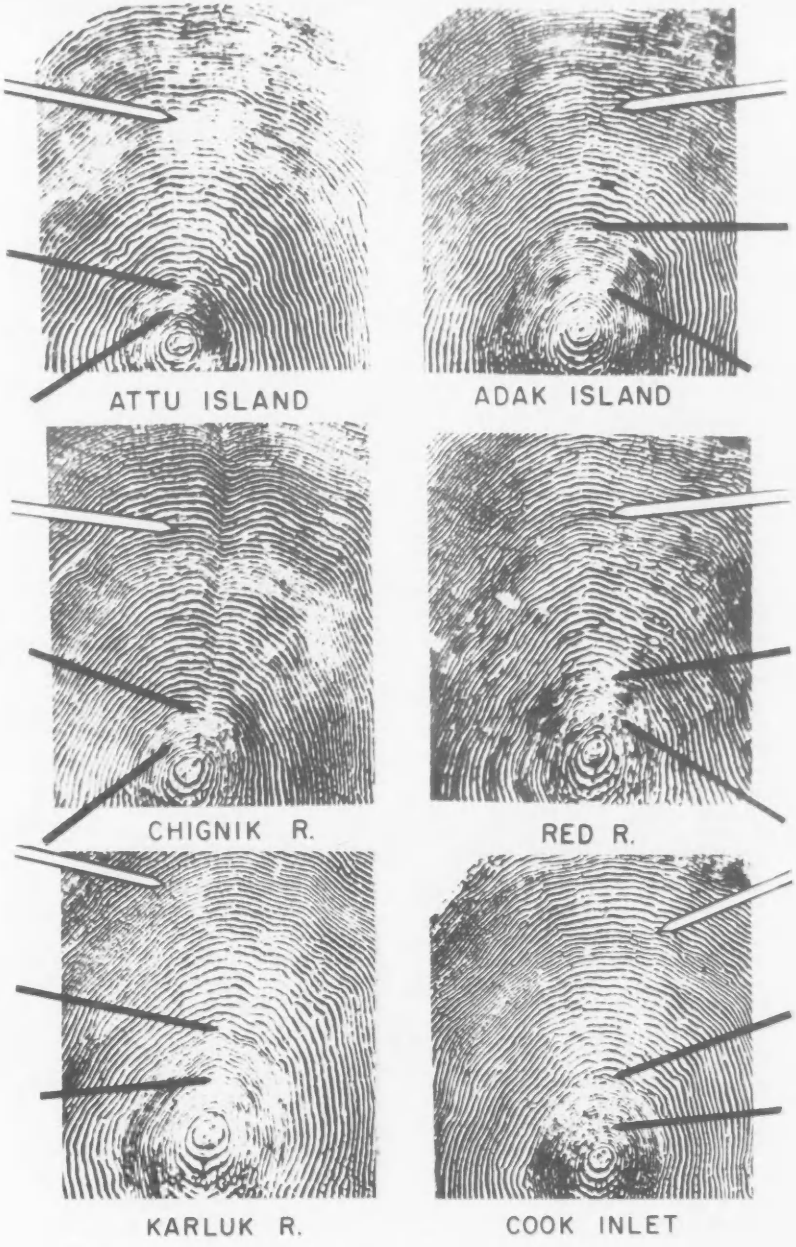

PLATE 12.—Age 2., Aleutian Islands to Cook Inlet.

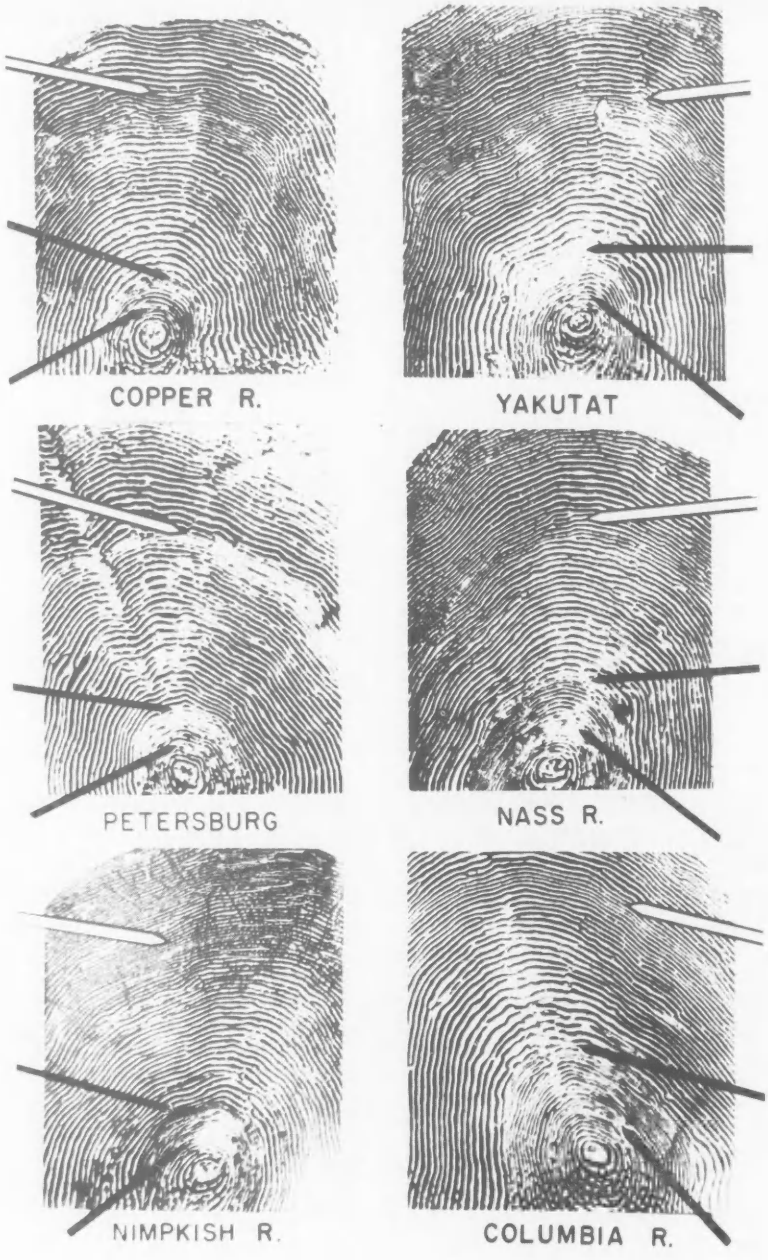

PLATE 13.—Age 2., Copper River to the Columbia River.

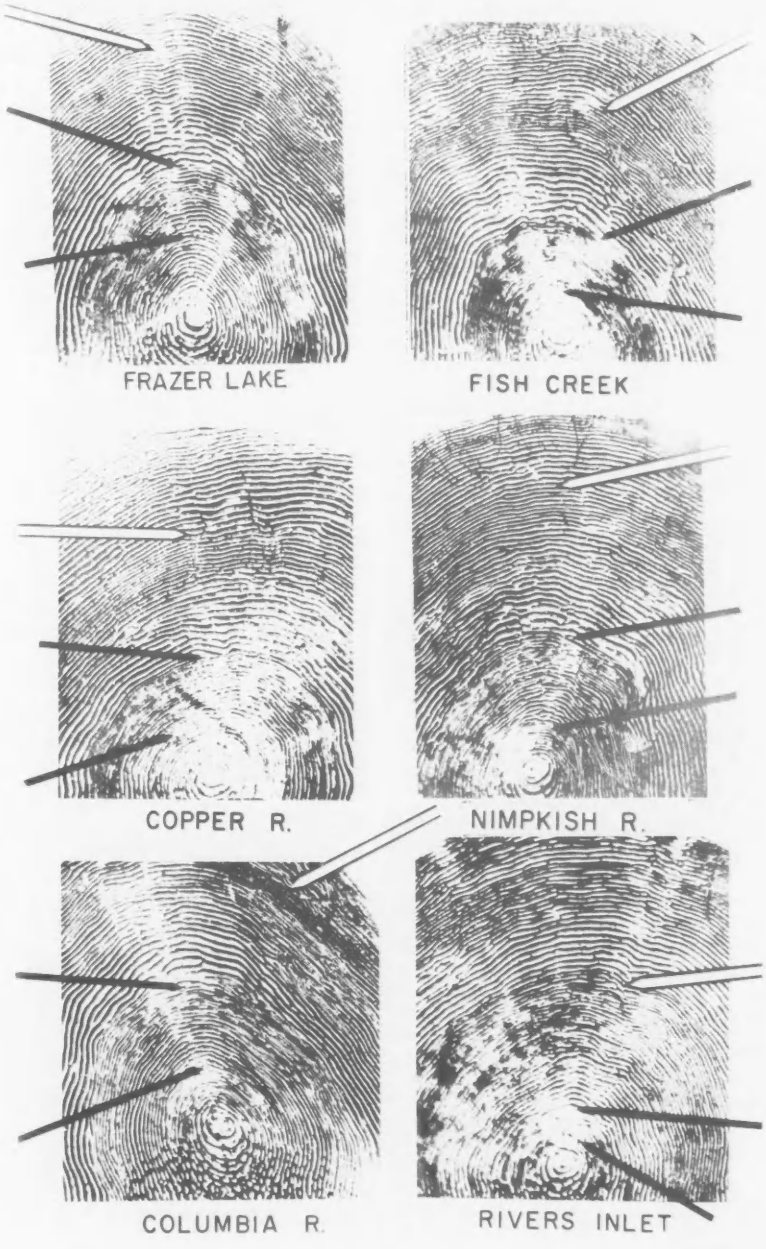

PLATE 14.—Age 2., North American areas with some distinctive scales.

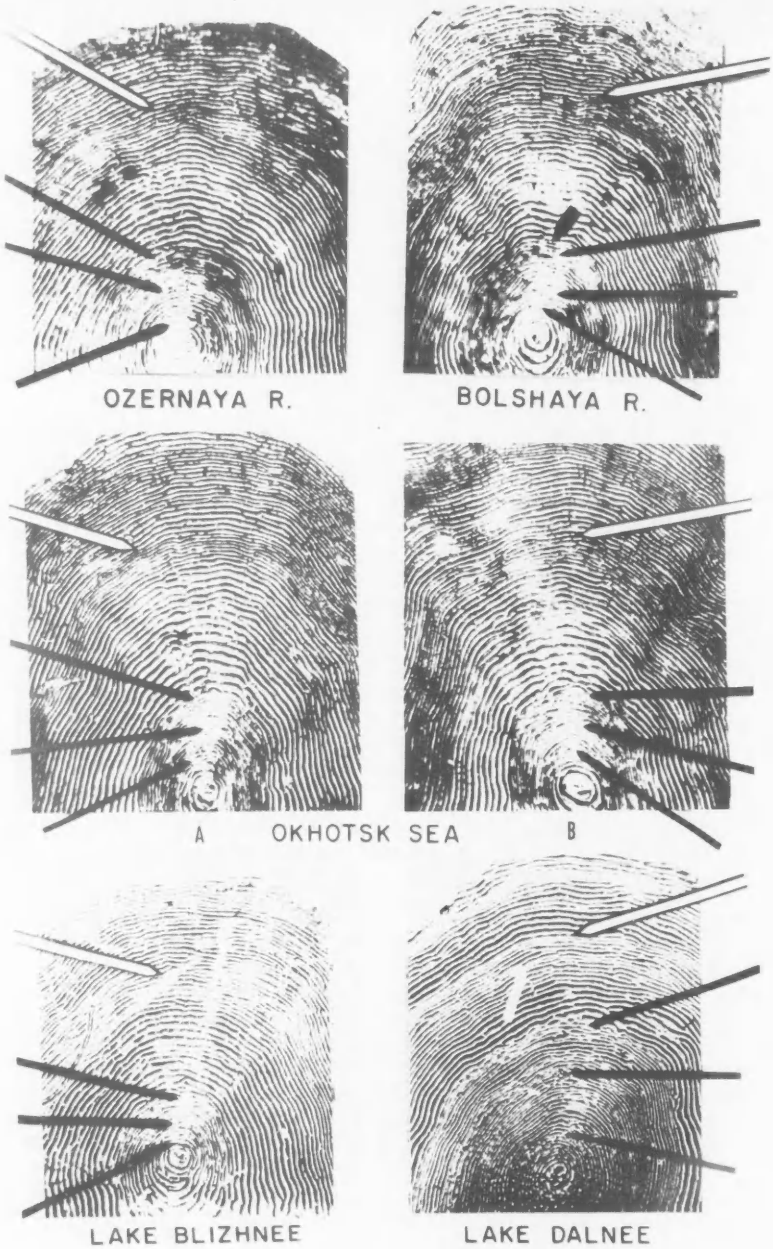

PLATE 15.—Age 3., Asia.

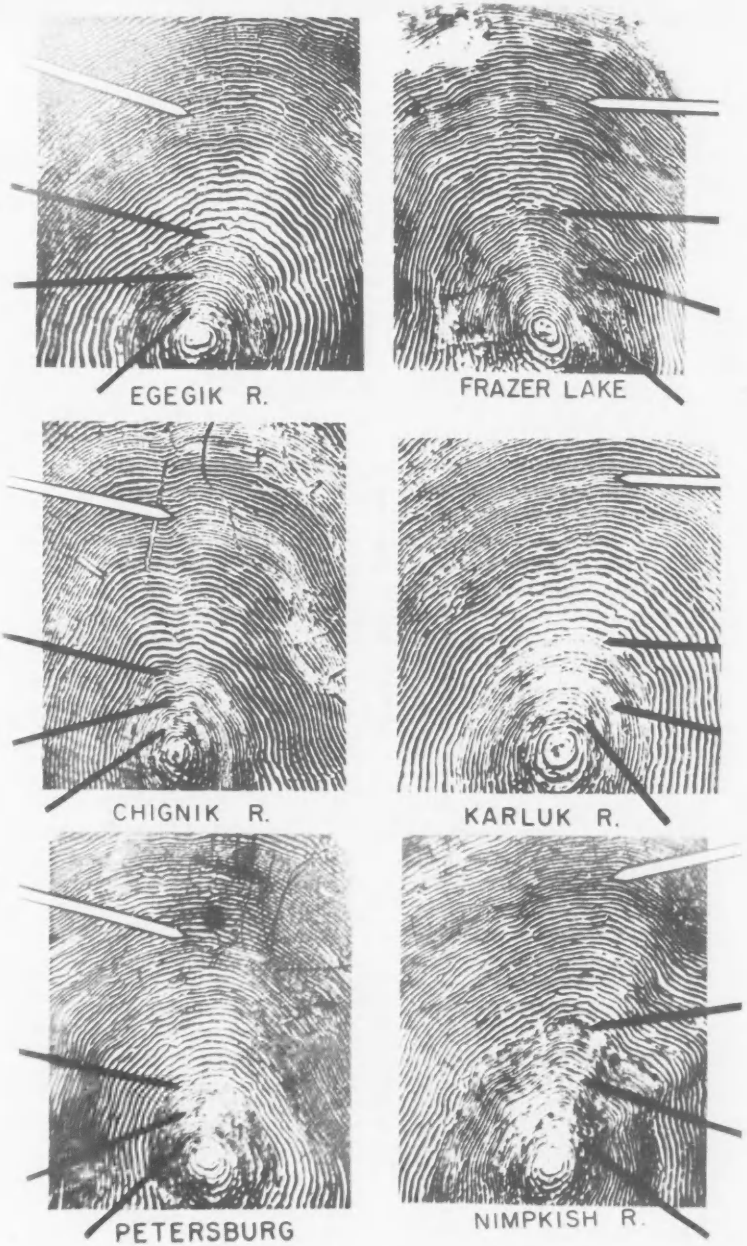

PLATE 16.—Age 3., North America, all areas.

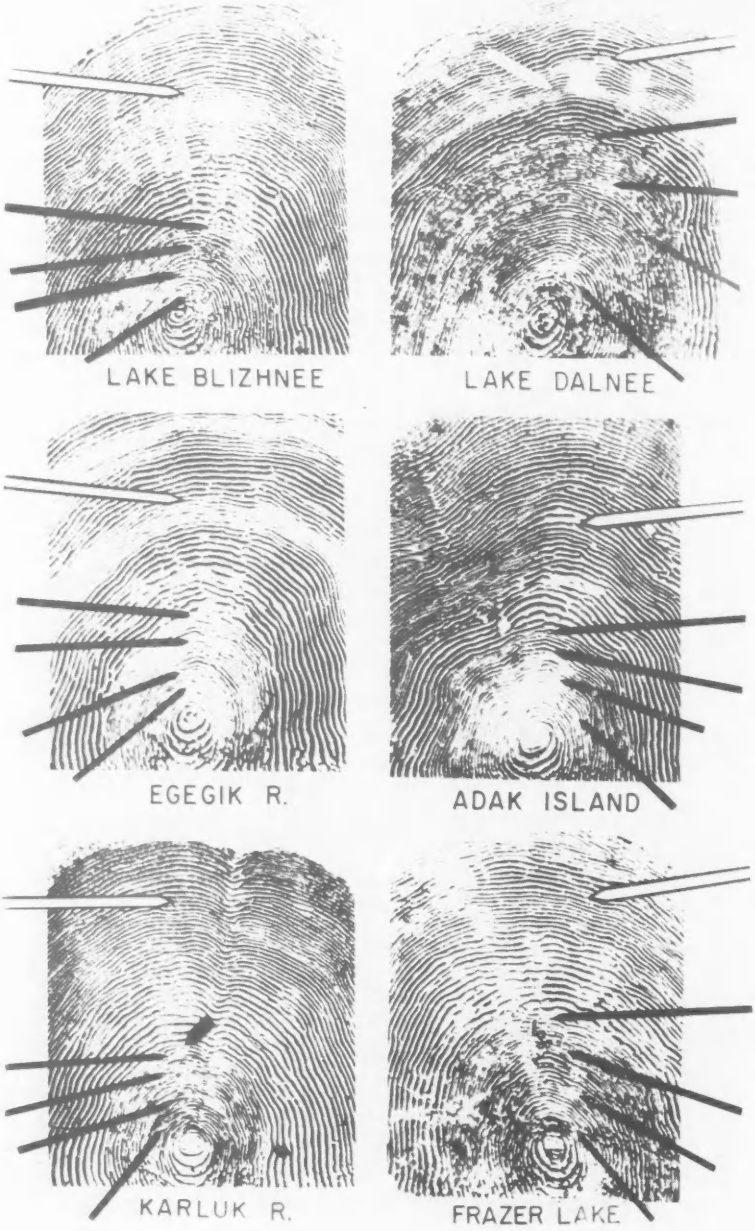

PLATE 17.—Age 4., all areas.

(1919) reported a stock spawning in the Harrison River, B.C., near its junction with the Fraser, B.C., and Krogius (1958) noted that they occurred in the Kamchatka, Bolshaya, and Paratunka Rivers, USSR. The Nushagak River, Bristol Bay, Alaska, had more than the usual number of individuals of this age in 1961 (Koo, 1962b) but not enough fish from which to take scales to furnish a frequency distribution.

Except for the Rivers Inlet, B.C., fish, there is little difference between areas in the features of the scales of this freshwater age. Scales from individuals taken from the Copper River, Alaska, southward to the Fraser River, however, tend to have a few more circuli in the first ocean zone than those from Bristol Bay, Alaska.

Fish of this age from Rivers Inlet and Smith Inlet, B.C., can be identified to that geographical area because the first ocean zone has the fine-textured circuli typical of most fish from these areas regardless of the freshwater age of the fish (see Plates 9 and 14).

AGE 1., 2., and 3., ALASKAN AREAS NORTH OF BRISTOL BAY (Plate 2; Tables 4, 5, 6, and 7)

Production of sockeye salmon north of Bristol Bay is small. The Kuskokwim River is the largest producer in the area. In the Norton Sound (Nome) and Kotzebue areas, few sockeye salmon are found. However, they are heavily exploited when present along with the other species—by local residents for food and barter—and thus are important in the local economy, especially in some years.

Very little is known of the migrations and ocean distribution of sockeye salmon originating in areas north of Bristol Bay. Of the many thousands of sockeye tagged by Japanese and United States scientists near the central Aleutian Islands, only two tagged near Attu Island in 1958 and one tagged near Kiska Island in 1960 have been returned from the area north of Bristol Bay. All three were recaptured in the Kuskokwim River (Hartt, 1966).

Presently it is not possible to identify the origin of most of the sockeye salmon from this area that are caught in offshore waters because the scales resemble those from many fish from Asia and Alaska Peninsula.

All freshwater age groups of sockeye salmon from north of Bristol Bay have small freshwater zones with few, often broken and irregular circuli in each zone. Some scales show plus growth (see Mosher, 1968, p. 251-254).

Circuli of the first ocean zone are widely and evenly spaced as in scales from Asian fish or those from the Alaska Peninsula. The widest spacing of circuli is usually some distance from the freshwater zone. The number of circuli varies from few, like fish from Bristol Bay, to somewhat more, like fish from Asia or Alaska Peninsula areas.

AGE 1., ASIA (Plate 3; Tables 4 and 5)

Scales from fish from the Kamchatka, Ozernaya, and Bolshaya Rivers do not differ much between rivers. The freshwater zone is relatively small with few, often broken and irregular circuli. Often adventitious checks (false winter marks, see p. 275, Mosher, 1968) occur in the freshwater zone of these scales. Scales that I have examined from fish captured in the Okhotsk Sea (which, according to Hanamura, 1966, may be a mixture of runs from the Ozernaya and Bolshaya Rivers and, at times, small numbers of fish from the Okhota and the Kukhtuy Rivers on the northern coast of the Okhtosk Sea and from other small producing streams of southeastern Kamchatka and the Kurile Islands) do not differ much from those of the Ozernaya and Bolshaya Rivers. Krogius (1958) reported that the scales of fish from the Kukhtuy River are similar to those of the Ozernaya River. Very few fish of this freshwater age are found in the Ozernaya River.

Scales from fish from the Paratunka River show two distinct types of freshwater growth; those from Lake Blizhnee have a very small freshwater zone with only a few, mostly broken, irregular circuli; those from Lake Dalnee have a moderately large to large freshwater zone with numerous regular, unbroken circuli. Krogius (1958) reported the favorable conditions for growth of the fish in Lake Dalnee and the much poorer conditions in Lake Blizhnee.

TABLE 9.—Freshwater scale characters of Asian stocks of sockeye salmon (from Krogius, 1958).

Item	Area and number of years in fresh water										
	1 year				2 years				3 years		
	Kamchatka River	Bolshaya River	Dalnee Lake	Blizhnee Lake	Kamchatka River	Ozernaya River	Dalnee Lake	Blizhnee Lake	Kamchatka River	Ozernaya River	Dalnee Lake
Type of circuli	Regular	Irregular	Regular	Irregular	Regular	Irregular	Regular	Irregular	Regular	Irregular	Regular
Years fresh water	*Number of circuli*										
1	10-16	5-10	12-23	9-15	5-10	5-8	6-23	9-13	5-8	5-8	5-15
2	--	--	--	--	10-24	9-13	10-24	5-9	5-8	5-8	5-15
3	--	--	--	--	--	--	--	--	5-8	5-8	5-15

The circuli of the first ocean zone of the scales from the Asian fish are average (some broken, some regular, see p. 255, Mosher, 1968) and more or less uniformly spaced. If there are a few more widely spaced circuli in the zone, they are usually some distance from the freshwater growth.

As can be seen from Table 3, my samples of scales from the Asian areas are quite small. Krogius (1958) reported on some of the scale characteristics of the Asian spawning stocks. Table 9 summarizes the pertinent material from her paper. My scale data generally agree with those she reported.

AGE 1., NORTH AMERICA

Bristol Bay (Plate 4; Tables 4 and 5)

The number and proportion of fish of this freshwater age group varies from year to year in the Bristol Bay rivers, but age 1. fish predominate each year in the Nushagak area as either the 1.2 or 1.3 age groups (Burgner, 1964).[6] Thus this is an important freshwater age group every year in Bristol Bay.

The bulk of the Bristol Bay sockeye salmon are produced in the Ugashik, Egegik, Naknek, Kvichak (including the Branch River), and Nushagak-Wood River systems. The relative importance of each river varies somewhat from year to year, but the Naknek-Kvichak area produces the largest number of fish, especially in the "big" years (see 1965 catch statistics in Appendix Table 1). In addition to these five river systems, there are a few other areas that provide some fish to Bristol Bay. Streams emptying into Togiak Bay and the Bear and Sandy Rivers on the north side of the Alaska Peninsula produce substantial numbers of sockeye salmon in some years. The Togiak area fish are usually of age 1., whereas those of the Bear River are of age 2. generally. The catches of the various areas of Bristol Bay for 1966, as an example, were as follows (International North Pacific Fisheries Commission, 1966):

Area	*Thousands of fish*
Naknek-Kvichak	5,397.6
Egegik	2,101.2
Nushagak-Wood River	1,170.3
Ugashik	445.4
Togiak	119.8
Bear and Sandy Rivers	151.3

Scales from fish of this age from Bristol Bay are quite similar between streams with only minor variations from year to year. Most scales have distinct freshwater and ocean zones with well-marked circuli. The freshwater growth is moderately large with well-spaced, regular, mostly unbroken circuli. Plus growth is sometimes present, especially in the Togiak, Nushagak, Kvichak, and Ugashik Rivers. In most cases it is easily identified on the scales.

The first ocean zone has relatively few circuli. The summer growth circuli are broad and widely spaced, predominantly regular, and unbroken. An area of widely spaced circuli is usually present near the freshwater zone. The ocean zones of scales of Bristol Bay fish have a more "open" appearance than those of fish from any other geographical area. This is the result of (1) a distinct winter zone of a number of closely spaced circuli, sometimes so close that the zone appears like a broad line around the scale (see winter

[6] Burgner, R. L. 1964. Age composition of Nushagak red salmon runs, 1946-63. Univ. Wash., Fish. Res. Inst. Circ. 219, 62 p. (Processed.)

marks labelled "1" on p. 260 of Mosher, 1968); (2) a relatively small number of circuli in the ocean zones; and (3) a wider spacing of the circuli usually near the freshwater zone.

In the other geographical areas, except Adak Island, there are more circuli, on the average, in the first ocean zone on the scales, and the winter zone may be diffuse (see winter marks labelled "3" on p. 260 of Mosher, 1968). These features result in a more even spacing of ocean circuli and a smaller average width per circulus producing a less "open" appearance. The effect of this characteristic is reflected in the size of the widest five adjacent circuli in the first ocean zone in the frequency tabulations shown in Table 10. This table shows that Bristol Bay scales, on the average, have five adjacent circuli that are substantially wider than on scales from fish of other geographical areas. This feature is found on scales of Bristol Bay salmon of all freshwater ages. Krogius and Krokhin (1956) also have noted variation in spacing of circuli.

Aleutian Islands to Cook Inlet (Plate 5; Tables 4 and 5)

The area from Chignik to Cook Inlet is an area of high production of Alaskan sockeye salmon, usually second to that of Bristol Bay. To provide a comparison with other areas, the commercial catch in 1966 of sockeye salmon in the subsections of this geographic area are shown below (International North Pacific Fisheries Commission, 1966):

Area	*Thousands of fish*
Aleutian Islands	1.0
South side Alaska Peninsula	606.2
Chignik	222.1
Kodiak Island	631.6
Cook Inlet	1,866.5

Commercial fishing operations in the Aleutian Islands and along the south side of the Alaska Peninsula take both transient fish migrating to Bristol Bay and local stocks (Atkinson, 1955). My samples from the Aleutian Islands, obtained for INPFC purposes, are of local stocks.

TABLE 10.—Frequency tabulations of the width of the widest five adjacent circuli in the first ocean zone of age 1. sockeye salmon from representative areas.[1] (Asterisks indicate modes.)

Width[2]	Asia[3]	Bristol Bay	Chignik	Cook Inlet	Fish Creek	Ketchikan	Skeena River	Rivers Inlet	Fraser River	Columbia River
13	--	--	--	--	--	--	--	1.5	--	--
14	--	--	--	--	--	0.5	--	5.9	0.3	--
15	--	--	--	0.3	--	1.5	0.9	12.4	2.8	0.3
16	--	--	0.3	0.9	0.3	6.5	5.4	20.6	8.3	1.5
17	--	--	1.4	2.9	2.7	16.5	12.2	25.9*	13.2	4.9
18	0.9	--	4.0	7.6	6.1	23.0*	16.8	20.0	16.7	11.0
19	3.2	0.2	9.1	13.1	9.1	20.0	19.0	8.8	18.4*	14.6
20	6.0	0.6	16.8	17.7	13.7	12.5	19.3*	2.9	16.7	15.2
21	8.8	2.0	21.3*	20.1*	18.0	8.5	15.1	0.9	12.1	16.8*
22	12.5	4.7	18.5	17.7	18.6*	5.5	7.1	0.3	6.6	15.5
23	15.7	7.8	12.5	10.8	14.0	2.0	2.3	0.6	2.8	11.3
24	16.7*	12.0	7.7	4.4	7.9	1.5	1.4	0.3	1.1	6.1
25	16.2	15.7	4.8	2.0	4.3	1.5	0.6	--	0.6	1.8
26	12.0	17.3*	2.8	1.2	2.7	0.5	--	--	0.3	0.6
27	5.6	15.7	0.9	0.6	1.8	--	--	--	--	0.3
28	1.9	10.9	--	0.6	0.6	--	--	--	--	--
29	0.5	6.3	--	0.3	--	--	--	--	--	--
30	--	3.5	--	--	--	--	--	--	--	--
31	--	1.8	--	--	--	--	--	--	--	--
32	--	1.1	--	--	--	--	--	--	--	--
33	--	0.4	--	--	--	--	--	--	--	--
No. in sample	54	281	88	80	82	50	88	85	87	82

[1] All samples from 1963 except Ketchikan, 1964.
[2] Millimeters of projected image, magnification 82×.
[3] Asian samples from an area near Southeastern Kamchatka coast where Asian fish are present almost exclusively (Margolis, Cleaver, Fukuda, and Godfrey, 1966). Data smoothed according to Henry (1961).

In the Aleutian Islands a number of scale types may be found. One type from Attu Island is similar to that of Asian fish: a small freshwater zone with few, often broken and irregular circuli. The first ocean zone of these Attu fish has evenly spaced, often broken circuli, but usually fewer circuli than the Asian fish. Another type, found in Unalaska Island samples in some years, has a larger freshwater zone with more circuli, like Bristol Bay fish (see submode at 17-18 circuli in column 8 of Table 4). A third type in both Adak and Unalaska Islands (see column 7 and primary mode in column 8 of Table 4) samples, has a large freshwater zone with numerous circuli like the Fish Creek sockeye salmon (these are pictured in Plate 8). Fish from Adak Island tend to have fewer circuli in the first ocean zone than fish from other areas. As noted above, the numbers of fish produced in the Aleutian Islands are very small, consequently these scale types are included here only to provide a complete series of age 1. scales.

Scales from Chignik, Kodiak Island, and most streams in Cook Inlet have moderately small freshwater zones with relatively few circuli (except those from Fish Creek, Plate 8), often with plus growth. Generally most of the fish from Kodiak Island are of ages 2. and 3. The first ocean zone of the fish from Chignik to Cook Inlet has a few more circuli on the average than do scales from Bristol Bay fish; moreover, the circuli are closer together and more uniformly spaced. The position of the widest circuli, if present, varies considerably in fish of this area group but often is near the following winter zone like many of the Asian fish.

Copper River to Southeastern Alaska (Plate 6; Tables 4 and 5)

The Copper River is the only river of significant production of sockeye salmon in this large geographical area; however, there are many streams that provide small numbers of fish to make a substantial total. The commercial catch for 1966 for subdivisions of this area follow (International North Pacific Fisheries Commission, 1966):

Area	*Thousands of fish*
Copper River	1,005.6
Yakutat	184.4
Southeastern Alaska	868.7

Fish of age 1. predominate here every year. Most fish from these areas are quite similar in both freshwater and first ocean circuli. The freshwater zone is small with few circuli. The freshwater zone of many fish taken near Petersburg and Ketchikan is very small with very few circuli, similar to that of the Rivers Inlet fish, but there are differences in the first ocean zone that distinguish Rivers Inlet scales. Most freshwater circuli of all fish of these areas are broken, irregular, crowded together, and poorly marked. Some scales show plus growth.

The first ocean zone of fish from these areas has a few more circuli on the average than do scales from Chignik or Cook Inlet. Circuli are usually irregular but evenly spaced; generally there is no area of wider circuli but sometimes there are a few wider circuli in two or more places in the first ocean zone. Adventitious checks (false winter marks) may also be present in the ocean zones. Thus some of these scales may be difficult to use for determination of age and racial origin.

British Columbia and the Columbia River (Plate 7, Tables 4 and 5)

This is also an area of high production of sockeye salmon. The yearly total for British Columbia varies, but it is either first or second to Bristol Bay in the total for North America. Average catches (from Aro and Shepard, 1967) for the major areas of British Columbia are as follows:

Area	*Millions of fish*
Nass River (average 1951-1963)	0.21
Skeena River (average 1951-1963)	0.49
Rivers and Smith Inlets (average 1951-1963)	1.06
Fraser River (average 1938-1963):	
1901 cycle	2.87
1902 cycle	6.12
1903 cycle	1.73
1904 cycle	1.92

Relatively few sockeye salmon are produced in the Columbia River (see Table 1). Fish of age .1

predominated in all sections of this geographical area; however, in some years age 2. fish may be abundant in the Nass River.

Most scales of fish from the rivers identified in this plate do not differ much between areas. (Scales from sockeye salmon from Rivers and Smith Inlets and some from the Nimpkish River are distinct and are shown on Plate 9.) Freshwater zones on the scales of fish from the Nass and Skeena Rivers tend to have slightly fewer circuli, and those from the Columbia River slightly more circuli than those from the Nimpkish and Fraser Rivers. (Scales from sockeye salmon from the Nimpkish River which are represented by the primary mode in column 20 of Table 4 are not pictured here as they are similar to the scales of Fraser River fish.) The freshwater circuli of scales from fish of these areas are mostly regular and unbroken. These characters give the freshwater zone a clear-cut appearance. Plus growth is often present.

The first ocean zone is usually distinct and well marked. There are numerous circuli in this zone, and even if some of them are irregular or broken, the zone usually has a clear-cut appearance. The spacing of circuli tends to be uniform, but a few wider spaced circuli may occur at any position within the zone. Scales from the Nimpkish River tend to have the most circuli of any of these areas. Adventitious marks are common in the ocean zones, but in spite of these irregularities, the circuli and winter marks are generally distinct and easy to count and measure.

Geographical Areas with Distinctive Scale Types (Plates 8 and 9)

There are two types of scales showing this freshwater age which are distinctive:

1. The "Fish Creek" type (Plate 8), so called because it was first observed in Fish Creek, Knik Arm, Cook Inlet, but later also found in small numbers in some other streams as noted below .
2. The "Rivers Inlet" type (Plate 9), so called because it was first observed in Rivers Inlet, B.C., but later found in some other areas, also noted below.

Fish Creek Type (Plate 8; Tables 4 and 5).— Fish Creek type scales are on most sockeye salmon from Fish Creek. A few were also found in the samples from Adak and Unalaska Islands and in the recently available samples from Frazer Lake (Kodiak Island) and the Nimpkish River (fish with more than 20 circuli in column 20, Table 4).

Fish Creek type scales are characterized by a large freshwater zone with many well-marked circuli. There is often a check or winter mark about 18 or 20 circuli from the center of the scale, followed by a few circuli of plus growth.

The circuli of the first ocean zone are also well marked, and in most cases, well separated, sometimes with an area of wider spaced circuli near the freshwater zone like most of the Bristol Bay fish. The numbers of circuli in this zone tend to vary with the locality from which the fish came: Adak and Unalaska Island, less than 22 circuli; Fish Creek and Kodiak Island, 22-27 circuli; and the Nimpkish River, over 27 circuli.

The annual number of adult fish with this scale type from all areas is relatively small (perhaps in the neighborhood of 100,000 fish as a maximum), but the scales have been observed in offshore samples because of their distinctive appearance (Mosher et al., 1961).

Rivers Inlet Type (Plate 9; Tables 4 and 5).— Gilbert (1914) first noted that scales of sockeye salmon from Rivers Inlet and later from Smith Inlet were different from those of other areas. Recently, samples from the Nimpkish River (on Vancouver Island, which empties into the northern end of Johnstone Straits near Rivers and Smith Inlets) became available. Some of these scales were also of the Rivers Inlet type.

These scales are characterized by a small, diffuse freshwater zone with very few circuli. Usually the circuli are broken, irregular, crowded together and difficult to count. The transition from freshwater to ocean growth is usually diffuse and difficult to distinguish.

The first ocean zone, the distinctive feature of these scales, has many uniformly spaced circuli, usually with no area of wider spacing. This first ocean zone often looks like freshwater

growth of scales from other areas (compare these photographs with those of the Fish Creek type on Plate 8). The second ocean zone is of typical ocean growth—heavy textured, well-spaced circuli. This zone, unlike that on scales from other areas, is usually wider than the first ocean zone. Often the winter check between the first and the second ocean zones is diffuse and indistinct.

The whole scale shows two large areas of contrasting texture: the freshwater and first ocean zones of fine-textured circuli and the second and subsequent ocean zones with coarse-textured circuli of typical ocean growth. On the scales from fish of other areas there is a difference in texture, but the zone of fine texture, the freshwater growth, is relatively small; and the coarse-textured portion of the scale, the entire ocean growth, is the major portion of the scale.

In the Nimpkish River, some of the fish of this age have scales of Rivers Inlet type (secondary mode at 12 circuli in column 20 of Table 4). These fish generally have a few more circuli in both the freshwater and first ocean zones than the fish from Rivers Inlet, and the circuli are also usually less broken and irregular than those from Rivers Inlet. The difference in texture, however, between the first and second ocean zone is typical of Rivers Inlet type scales.

Most of the fish from Rivers and Smith Inlets have scales of this type. In representative samples the following typical Rivers Inlet scales were found:

(Area and year)	*Percentage of Rivers Inlet type*
Rivers Inlet, 1958	126 of 156 fish (76.2%) (Manzer, Bilton, and Mosher, 1960)[7]
Rivers Inlet, 1963	374 of 377 fish (98.4%)
Smith Inlet, 1960	123 of 132 fish (93.2%)
Smith Inlet, 1961	246 of 270 fish (91.1%)

These percentages approximate the range of typical Rivers Inlet type scales in this area. The few scales that are not typical of fish of these areas usually resemble scales of the Skeena or Nass Rivers; consequently they still are in British Columbia.

Only an occasional scale from the other areas (Cook Inlet to the Fraser River) has the appearance of a Rivers Inlet scale. In these few cases, the number of circuli in the first ocean zone is usually less than that of the Rivers Inlet fish.[8]

In a test of 300 unlabeled scales from many areas over the range of the species set up by an assistant, I correctly identified 63 out of 64 Rivers Inlet scales. This indicates that these scales are indeed distinct and can be identified from their appearance with a high degree of accuracy.

The Rivers Inlet area is a good producer of sockeye salmon. In most years more than 1 million fish are caught there. The Nimpkish River is a small producer, but escapements of 150,000 and 70,000 fish were recorded in 1957 and 1958, respectively (Henry, 1961).

Rivers Inlet type scales have been observed widely in offshore samples (Manzer et al., see footnote 7; Mosher et al., 1961).

AGE 2., ASIA (Plate 10; Tables 6 and 7)

Representative scales of sockeye salmon from the Kamchatka, Ozernaya, and Bolshaya Rivers, the Okhotsk Sea, and Lakes Blizhnee and Dalnee are shown on this plate. Like those of age 1., scales from these fish, except Lakes Blizhnee and Dalnee, do not differ much between areas. The freshwater zone is of moderate size, sometimes with plus growth. The circuli are close together and many are broken or irregular. (See Table 9 for a summary of freshwater scale characters of Asian sockeye salmon from Krogius, 1958.)

The first ocean zone of scales from these fish also do not differ significantly and are similar to the same zone of the scales of the age 1. fish from the same areas. Usually the circuli are evenly and moderately closely spaced and lack the open

[7] Manzer, J. I., T. H. Bilton, and K. H. Mosher. 1960. The ocean distribution of sockeye salmon originating in Rivers and Smith Inlets. Fish. Res. Board Can. (Nanaimo, B.C.) and Bur. Commer. Fish. (Seattle, Wash.) (INPFC Doc. 407), 5 p. (Processed.)

[8] From this point on, the term "Rivers Inlet" also includes Smith Inlet and the Rivers Inlet type scales of fish from the Nimpkish River.

appearance of the Bristol Bay scales. An area of wider spaced circuli may often be found at any position in the first ocean zone, but usually it is near the middle of the zone or the following winter zone. Plus growth is sometimes present.

Scales of many fish from Lake Blizhnee are distinctive. They have a very small freshwater zone with few circuli in each year's growth. Circuli are irregular and the zone is difficult to interpret because of the broken and closely spaced circuli. The first ocean zone is similar to that of the other Asian fish of the Ozernaya, Bolshaya, and Kamchatka Rivers.

Scales from Lake Dalnee fish have large to very large freshwater zones. The freshwater growth makes up a larger portion of these scales than those from any other locality over the range of the species. The circuli of both the freshwater and ocean zones are usually regular and well marked. Sometimes there are fewer circuli in the first ocean zone than on scales from other Asian areas. Scales of fish of this freshwater age can be easily identified as being from Lake Dalnee when they are encountered in samples of fish taken from the North Pacific and Bering Sea because of the unusually large freshwater zone (Mosher et al., 1961).

AGE 2., NORTH AMERICA

Bristol Bay (Plate 11; Tables 6 and 7)

The number of fish of this freshwater age varies from year to year in the different rivers, but few are ever found in the Nushagak and Togiak areas. In some years of large production in Bristol Bay most of the fish are of age group 2.2.

As was true of age 1. fish from Bristol Bay (Plate 4), most scales from these fish, including Bear River, do not differ much between streams. Freshwater and ocean circuli are regular and clear cut. The freshwater zone is moderately large to large, and well marked; the circuli are generally well separated, and plus growth is often present. There are relatively few, well-separated circuli in the first ocean zone. In most cases the winter marks are distinct. Usually the widest circuli are near the freshwater zone. Because the first 5 or 10 circuli of each ocean growth zone usually are widely separated and the winter marks are well marked and compact, the scales have a more open appearance than scales of fish from other geographical areas. Taken as a whole, scales from Bristol Bay fish are easier to interpret than sockeye scales from other geographical areas.

Aleutian Islands to Cook Inlet (Plate 12; Tables 6 and 7)

Fish of age 2. are usually abundant in this area. Diverse types are present. Aleutian Islands (typified by Attu Island) and Chignik River fish have a small freshwater zone with irregular circuli much like the Asian sockeye salmon. Fish from Unalaska Island (not pictured), Red River (Kodiak Island), and Cook Inlet have moderate-sized freshwater zones with more irregular and broken circuli on their scales than Bristol Bay fish, but fewer than the Asian fish. Adak Island and Karluk River (Kodiak Island) fish have large, usually clear-cut, freshwater zones on their scales, also with more irregular circuli than those from Bristol Bay.

As is true with the age 1. fish, Adak Island sockeye salmon have the fewest circuli in the first ocean zone of their scales; those from Unalaska Island have about the same distribution of circuli as the Bristol Bay fish; and those from Attu Island and from the Alaska Peninsula to Cook Inlet have somewhat more circuli than fish from Bristol Bay. The circuli in the first ocean zone are generally closer together than on scales from Bristol Bay fish. The area of widest circuli, if present, may occur at any position within the growth zone, but it is often near the following winter ring, such as occurs with many Asian fish. Many of the scales from this area, especially from the Aleutian Islands and Chignik, are difficult to interpret with confidence.

Copper River to Columbia River (Plate 13; Tables 6 and 7)

In this large area relatively few age 2. sockeye salmon are produced. In fact only in some years in the Nass River are there substantial numbers.

There are, however, a number of different scale types among those that do occur.

Most fish from the Copper River, Yakutat, and Petersburg areas have scales much like those of Chignik and Cook Inlet. The scales are characterized by small- to medium-sized freshwater zones in which most of the circuli are broken or irregular. The first ocean zone of these scales averages slightly more circuli than those of the Cook Inlet area, however, and the circuli are more closely and evenly spaced.

A second type of scale from this area has a large freshwater zone with numerous circuli. These scales are found in small numbers in various areas from the Copper River to the Columbia River and are shown in Plate 14.

Scales showing this freshwater age from the Nass, Skeena, and Fraser Rivers and some from the Nimpkish River (the British Columbia fish) usually have moderately large, well-marked freshwater zones. Usually the broken circuli are confined to the winter checks. In the first ocean zone, fish from the Nimpkish River have more numerous, regular, evenly spaced circuli than those from any other area. Scales of these British Columbia fish are relatively easy to interpret and often differ from Bristol Bay scales only in having, on the average, a few more circuli and more evenly spaced circuli in the first ocean zone. The scales tend to have a less open appearance than those of Bristol Bay fish.

The few scales of this age group of sockeye salmon from the Ketchikan area occur in at least three types: (1) scales like those of the Copper River-Petersburg area, like the one pictured on this plate from a fish taken near Petersburg, (2) scales with a larger freshwater zone like those from Nass River fish, and (3) very few scales with very large freshwater zones like the one pictured from the Copper River on Plate 14. In the Ketchikan area there are many small streams that produce some sockeye salmon. In addition, many channels and bays serve as waterways through which fish migrate to other areas. Thus it is possible that many of the Petersburg and Nass type scales taken in this area may actually be from fish migrating to the Petersburg area or the Nass River.

Most fish of this age found in the Columbia River have large freshwater zones varying from those like the one pictured on this plate to ones with very large freshwater zones, shown on Plate 14. On all of these Columbia River scales, the freshwater circuli are well marked and well separated, even if many are broken or irregular. The circuli of the first ocean zone of these scales are also usually well marked; they are evenly and widely spaced. The zone averages somewhat fewer circuli than on scales from the Nimpkish, Nass, Skeena, and Fraser Rivers but more than on the scales from Bristol Bay fish. An area of wider spaced circuli may occur at any position within the first ocean zone, but the difference between the widely spaced and the closely spaced circuli is not as great as in the Bristol Bay scales.

Fish of this freshwater age are rare in Rivers Inlet. These scales can be identified as typical Rivers Inlet type from their appearance (see Plate 14).

Areas with Some Distinctive Scales (Plate 14)

In most years a number of areas from Kodiak Island to the Columbia River have some fish with very large freshwater zones on their scales, but except for the Nimpkish River, there were not enough fish to provide data for frequencies of the number of circuli. Only slight differences in the freshwater zone of the fish from the various areas can be found.

In some years, scales from some Bristol Bay and Aleutian Island fish may also have these very large freshwater zones.[9] These are not pictured on this plate because they resemble the ones shown from the Copper River to the Columbia River, and they do not occur in most years.

Differences in the number and character of the circuli in the first ocean zone of the scales from fish of the different areas, however, offer an indication of the locality from which the fish came. The largest number of circuli in this zone tends to be on scales of the Nimpkish River sockeye salmon; fewer circuli (and more broken

[9] A number were observed in Bristol Bay samples for 1970.

circuli) are found on the scales from Ketchikan, Petersburg, Copper River, and Columbia River fish; even fewer circuli (and fewer broken circuli) are found on the Fish Creek and Kodiak Island fish, whereas the least number of circuli (and the most complete and regular circuli) are found on the scales from Aleutian Island and Bristol Bay fish.

The reasons for some of the fish from these areas having such a large freshwater growth zone is a subject for future research. The numerous streams and tributaries of the larger river systems encompass a wide range of environmental conditions. It is likely that these fish are spawned and grow in nursery areas with excellent conditions for freshwater growth. In some years the growth conditions in certain streams may be better than in other streams, contributing to the year to year variation in numbers of fish with this scale type.

In Rivers Inlet, sockeye salmon with scales showing this age are rare. The scales of the few fish that have been found, however, are of typical Rivers Inlet appearance: a small freshwater zone with only a few (mostly broken) circuli in each year's growth, a fine-textured first ocean zone with numerous circuli, and a second (and subsequent) ocean zone of typical ocean type circuli. Thus the scales show the two large areas of contrasting texture, like those of Rivers Inlet scales of other ages—Plates 1 and 9. (Note how much the scale area to the end of the first ocean zone, white arrow, resembles the freshwater zone of the Columbia River scale on this plate.)

AGE 3., ASIA (Plate 15; Tables 8a and b)

Usually fish of this freshwater age are in substantial numbers only in the Asian areas and in Kodiak Island streams, but a few are also found each year in Bristol Bay, especially in the Egegik and Naknek Rivers.

On the Asian side of the Pacific Ocean, scales from fish of the Ozernaya, Bolshaya, and Kamchatka Rivers and the Okhotsk Sea do not differ much (column 1 of Table 8 shows data from fish taken off the southeast coast of the Kamchatka Peninsula where a number of Asian stocks intermingle). The scales of most Asian fish, except those from Lakes Blizhnee and Dalnee, have relatively small freshwater zones with only a few circuli in each year's growth. Many of the circuli are irregular, broken, and closely spaced. The first ocean zone of these scales is like that of the age 1. and 2. fish from the same geographical areas. There are a few more circuli present on the scales of these fish than on those from Bristol Bay, and the circuli are generally uniformly spaced. An area of wider spaced circuli may be present in the first ocean zone, but it generally is less pronounced than on scales from Bristol Bay fish.

Fish of this age are also found in Lake Blizhnee. The scales have a very small freshwater zone with very few circuli in each year's growth. The first ocean zone of these Lake Blizhnee fish is also like that of the other Asian fish except those from Lake Dalnee.

Fish of this freshwater age are relatively common in Lake Dalnee. The scales are distinctive: a very large freshwater zone with numerous, usually clear-cut circuli. The freshwater zone makes up a larger portion of the scales of fish from Lake Dalnee than of fish from any other area in Asia or North America. As in age 2. and 4. fish, the first ocean zone often had fewer circuli than usual for Asian fish—sometimes even fewer than on scales from Bristol Bay or Adak Island fish.

AGE 3., NORTH AMERICA (Plate 16; Tables 8a and b)

As noted above, Kodiak Island has the most sockeye salmon of age 3. on the American side of the Pacific Ocean. In some years a major portion of the run to the Karluk River may be of individuals of this freshwater age with 2 or 3 winters in the ocean (the 3.2 and 3.3 ages). In most years substantial numbers of age 3. fish are found. The freshwater zone of the scales of these fish is relatively large; the circuli are well separated and usually well marked, although more of the circuli may be irregular or broken than on most Bristol Bay scales. The first ocean zone is also well marked; the circuli are distinct and often widest near the freshwater zone as in

the scales of fish from Bristol Bay. Usually a few more circuli are found than on Bristol Bay or Asian scales.

Bristol Bay scales of this age (Egegik River shown) look like Bristol Bay scales of age 2. with an additional freshwater winter mark. The freshwater zone is moderately large and distinct; the circuli are well marked. Circuli of the first ocean zone are also distinct and are fewer in number than on scales from fish of other North American areas except Adak Island. The circuli are usually widely separated near the freshwater zone. These scales, like those from fish of the other Bristol Bay age groups, are usually easy to interpret.

Fish of this age are rarely found in other North American areas. Scales from these age 3. sockeye salmon resemble those of age 2. from the same area but have an additional winter mark in the freshwater zone. Thus, usually the freshwater zone is large (Nimpkish River shown). In Chignik and southeastern Alaska (Petersburg shown) where small freshwater zones predominate, occasionally a fish with a very small freshwater zone with three distinct winter marks may be found.

Among fish of this age, the number of circuli in the first ocean zone is similar to that of age 1. and 2. fish from the same area; thus the number of circuli in the first ocean zone can indicate the area of origin of the fish.

AGE 4., ALL AREAS (Plate 17)

Scales that show this age are rare from Asia to Cook Inlet, Alaska, and are almost never observed in areas southeast of Cook Inlet. Insufficient numbers of fish of this age group have been obtained to assemble frequency distributions of the number of circuli on the scales of fish from any area. While it is possible that some of these scales may be younger with accessory checks, the spacing and appearance of the markings suggests that most of them are actually age 4.

It appears from the scales which I have seen that the freshwater and ocean zones are similar to those found on scales of fish of age 2. and 3. from the same geographical areas, with additional winter marks in freshwater, and consequently somewhat larger freshwater zones. For instance, the scales of fish from Lake Dalnee have an enormous freshwater zone, and relatively few circuli in the first ocean zone. The Lake Blizhnee fish of this age, on the other hand, have scales with a small freshwater zone with relatively few circuli in each year's growth and with approximately the same number of circuli in the first ocean zone as would be found in most Asian fish of age 2. or 3.

Fish of the Aleutian Islands show two different types of scales. One type (similar to Lake Blizhnee scales) has an extremely small freshwater zone with few circuli in each year's growth. Scales of this type have broken and irregular circuli in both the freshwater and ocean zones, as on the scales of many Asian fish. They average fewer circuli in the first ocean zone than Asian fish, however, and often average fewer circuli than on scales from Bristol Bay fish. The second type, illustrated by a scale from Adak Island, is similar to scales of fish of the same age in Bristol Bay (Egegik River shown). The freshwater zone is moderately large with numerous circuli, some of which are irregular or broken. The first ocean zone has circuli like scales of age 2. fish from the same locality. Generally the circuli are well marked and more widely spaced near the freshwater zone.

Scales from Kodiak Island (illustrated by scales from Karluk River and Frazer Lake) have freshwater zones that vary from large to extremely large.

DETERMINATION OF ORIGIN OF SOCKEYE SALMON TAKEN IN OFFSHORE WATERS

This section is not a formal key for classifying sockeye salmon by stock or geographic origin. The purpose of this section is to show how age and scale characteristics illustrated in the previous section of the paper can be used by experienced workers to assist in identifying the most probable area of origin of many sockeye salmon taken in offshore waters.

Scales of fish from different offshore areas re-

quire different considerations for study. The following discussion is divided into two parts for purposes of racial identification of the fish:

1. The area westward of long 175° W in the North Pacific Ocean and Bering Sea.
2. The eastern North Pacific Ocean and Gulf of Alaska.

WESTERN AND CENTRAL NORTH PACIFIC AND BERING SEA

Studies of the distribution of sockeye salmon stocks in central North Pacific and Bering Sea for the INPFC, including the morphological, parasitological, and tagging reports noted in the introduction, as well as the scale studies of Mosher (1963) and Mason (1966, 1967a, 1967b) have shown intermingling of stocks primarily from Asia and Bristol Bay over most of the offshore area westward of long 175° W to between 160° and 170° E, depending on the latitude (see Figure 74 of Margolis et al., 1966).

When examining scales of fish from this area, occasionally a scale with a very large freshwater zone may be seen. These scales usually stand out distinctly from others and are most likely from Lake Dalnee fish (Plates 3, 10, 15, and 17). A few scales, however, may be seen with unusually small freshwater zones. These scales are most likely from fish from Lake Blizhnee (Plates 3, 10, 15, and 17).

Aside from these scales with unusually large or small freshwater zones, nearly all of the scales are of two types: (1) Bristol Bay type scales (Plates 4, 11, 16, and 17)—well-marked scales with regular circuli in all growth zones and a moderately large freshwater zone, usually with less than 23 circuli in the first ocean zone. The widest spacing of circuli in the first ocean zone (and often the other ocean zones as well) is usually near the freshwater zone. The ocean portion of these scales has an open appearance. (2) Asian type scales (Plates 3, 10, 15, and 17)—relatively small freshwater zones with many broken or irregular circuli. The first ocean zone usually has 23 to 26 circuli which are widely spaced over the whole summer growth portion but lack the open appearance of the Bristol Bay scales. The ocean zone of these fish often has three and sometimes four winter marks.

EASTERN NORTH PACIFIC OCEAN AND GULF OF ALASKA

When we examine scales of fish taken eastward of long 175° W and in the Gulf of Alaska, many types may be encountered. At the present state of knowledge, I believe that determination of origin is extremely difficult or impossible if separation by each individual stream or river within the area is required. If, however, determination by general locality of origin and certain areas is the immediate goal, age and scale characteristics can be used to classify many, if not most, of the fish.

No sockeye salmon tagged in the Gulf of Alaska has ever been returned from Asian coastal streams.[10] Numerous sockeye tagged in other areas and other species tagged in the Gulf of Alaska have been returned from Asian coastal rivers. Considering that many thousand sockeye salmon have been tagged in the Gulf of Alaska, at least a few should have been recaptured from Asian waters if any Asian fish were present there during the time of tagging.

Thus, the Asian stocks need not be considered when dealing with fish taken in the Gulf area. Some of the scales of fish taken from the Alaska Peninsula eastward to southeastern Alaska resemble Asian fish in some characters at least. This similarity to Asian fish in scale characters has been noted by Oseko (1961),[11] and in morphological characters, by Fukuhara et al. (1962). Consequently any scales encountered in the Gulf of Alaska samples that resemble those from

[10] One fish tagged at 48°29′ N, 159°10′ W in the area south of the Gulf of Alaska in 1961 was recovered the same year off the Kamchatka coast at 50°47′ N, 162°29′ E. Kondo et al. (1965) concluded that it was not possible to draw any definite conclusions from the recovery. Margolis et al. (1966), however, considered it a Kamchatka sockeye salmon.

[11] Oseko, M. 1961. Certain characteristics of the growth pattern of scales as a means of discriminating between sockeye salmon from various streams of Alaska and the Kamchatka Peninsula. [In Japanese.] Hokkaido Reg. Fish. Res. Lab. (INPFC Doc. 479). 38 p. of Japanese text; 5 p. of preliminary English translation. (Processed.)

Asian fish can be considered of North American origin and classified accordingly.

In the area east of long 175° W into the Gulf of Alaska, the number of circuli and the general appearance of the freshwater and first ocean zones of most scales of age 1. fish can be evaluated and the most probable area of origin can be determined by comparison with the scales in Plates 4 to 7.

Rivers Inlet scales can be identified easily by their appearance. They stand out distinctly from the scales of other areas in all freshwater ages because of the fine-textured circuli of the freshwater and first ocean zones (Plates 1, 9, and 14).

Some scales may be found that have large freshwater zones. In age 1. these are most likely from Unalaska or Kodiak Island, Fish Creek, or the Nimpkish River (Plate 8). In age 2., they may be from Kodiak Island, Fish Creek, Copper River, the Ketchikan area, the Nimpkish, Fraser, or Columbia Rivers (Plate 14). None of these stocks are abundant in these ages, but some are taken at times. The number of circuli in the first ocean zone may assist in determining from which specific area the fish originated.

Migration routes to the various streams have not yet been determined for most stocks, but certain indications are given by tagging studies. Research by the Canadians for the INPFC (Fisheries Research Board of Canada, 1967a, 1967b) shows that fish recovered in the Rivers Inlet-Fraser River area tend to have been tagged farther southward in the Gulf of Alaska in spring and summer than those recovered from the Cook Inlet and Copper River areas. Fish recovered from Bristol Bay tend to have been tagged farther westward than those recovered from the Rivers Inlet-Fraser River areas. Hartt (1962, 1966) and Kondo et al. (1965) indicated that many Bristol Bay fish move westward along the south side of the Alaska Peninsula and the Aleutian Islands, turn north through the passes, and then migrate eastward into Bristol Bay.

Thus if the scale (age 2.) under study has a large freshwater zone and a large number of circuli in the first ocean zone (over 27 circuli) and was taken in the southern part of the Gulf of Alaska, it would be most likely from the Nimpkish River (Plate 14). If the scale had 23 to 27 circuli in the first ocean zone and was taken in the northern part of the Gulf, it would probably be from Cook Inlet, Kodiak Island, or Fish Creek; if it had 28 to 30 circuli, it would probably be from the Copper River or southeastern Alaska (Plate 14); and if it had less than 23 circuli, it would probably be from a Bristol Bay fish (Plate 11), or possibly from a spawning stream on Adak or Unalaska Island (Plate 12)) if caught near the Aleutian Islands.

In age 3. sockeye salmon, a scale with a large freshwater zone and about 26 circuli in the first ocean zone indicates most likely a Kodiak Island fish; less than 23 circuli, Bristol Bay or Unalaska Island origin; and over 30 circuli, Nimpkish River origin (Plate 16). A scale with a very small freshwater zone and 25 to 28 circuli in the first ocean zone indicates a fish probably from the Copper River or southeastern Alaska (Plate 16).

In age 0. fish, aside from the Rivers Inlet fish which are distinguishable by their compact, fine-textured first ocean zone (Plate 1), the number of circuli in the first zone offers the best indication of area of origin: a few circuli (20 to 25), Bristol Bay; a large number (over 34), southeastern Alaska southward; or an intermediate number (26 to 34), the area from Bristol Bay to southeastern Alaska (Plate 1).

In age 4., any fish found in the Gulf of Alaska will most likely be from Kodiak Island (Plate 17). If the scale is from a fish taken near the Aleutian Islands and has relatively few circuli in the first ocean zone, it may be from a stream on Attu or Adak Island (Plate 17) or from Bristol Bay.

South of lat 50° N in the southern Gulf of Alaska, the intermingling of stocks may be complex. Very few fish have been tagged in this area; catches are very small as a rule, and consequently little is known about these fish. Study of their scales offers the best means of identifying their origin and determining other features of their life history.

Evidence from fishing by United States, Japanese, and Canadian research vessels south of lat 50° N in the late autumn, winter, and early spring indicated that sockeye salmon of many stocks may be present over a wider area to the

southward than during May and June when most fishing has been carried on.[12]

Kondo et al. (1965) show the estimated area of distribution of sockeye salmon in May and June. In the area between long 165° and 175° W, they show only Bristol Bay and Gulf of Alaska stocks (not quite to 170° W). Thus in the area between long 170° and 175° W, probably only Bristol Bay (Plates 1, 4, 11, 16, and 17), Alaska Peninsula, and Aleutian Island stocks (Plates 5, 12, 16, and 17) will be present in most years.

These procedures have been the result of intensive study of sockeye salmon scales from 1954 to 1971. In addition I have examined collections taken before 1954 (Bristol Bay, from the early 1920's; Karluk River, from the mid-1940's; Copper River, from the mid-1930's; the Petersburg area, from the late 1940's; and the Columbia River, selected years from 1910 to 1922) and have verified the scale characters pictured and described here. Although there are minor differences from year to year, within and between areas, the characters have been relatively stable over a long period of time. The pictures of Rivers Inlet scales shown in Gilbert (1914) resemble the Rivers Inlet sockeye salmon scales of recent samples. Thus the pictures and descriptions shown in this report are representative of scales from fish of these areas and can be used as guides in determining the racial origins of fish taken in offshore areas of the North Pacific and adjacent seas.[13]

[12] I have examined the few scale samples available from the area south of lat 50° N and eastward of long 175° W and have observed many diverse scale types. This leads me to believe that fish from many sources intermingle there: some fish from Bristol Bay, the mainland areas around the Gulf of Alaska, and even from Asia.

[13] Study of salmon scales, in common with other fish scales, is a specialized branch of fishery biology. It requires a person with a special temperament: one who can sit in a darkened room, often for hours at a time, involved in routine counting and measuring of scale features. It requires a person who can evaluate the subtle differences between scales and not be overcome by them. Consequently, a sympathetic approach and a certain amount of experience with fish scale study is required to be able to use scale characteristics to determine the racial origins of sockeye salmon. When a scientist has obtained this experience and can evaluate the differences among scales, he will find that the information available through study of the scales can be applied toward answering many questions of the life history of the individual fish in addition to its age and racial origin.

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APPENDIX TABLE 1.—Commercial catch of sockeye salmon, 1964 to 1968.

Area	1964	1965	1966	1967	1968
			Thousands of fish		
Asia	8,143.5	13,677.2	8,817.5	10,753.6	8,966.7
Japan	7,175.0	12,171.0	7,667.0	9,783.0	8,131.0
USSR	968.5	1,506.2	1,150.5	970.6	835.7
North America	14,135.7	34,115.8	20,496.8	17,513.6	15,343.4
Canada (B.C.)	3,619.0	3,019.4	4,020.3	6,743.0	6,266.0
United States	10,517.7	31,096.4	16,476.5	10,770.6	9,007.4
North of Bristol Bay	13.4	12.9	1.1	1.3	5.9
Bristol Bay	5,825.7	24,718.7	9,559.5	4,555.4	3,030.0
Alaska Peninsula	1,427.3	1,857.2	1,460.9	1,074.0	2,341.7
Cook Inlet	990.7	1,424.4	1,866.5	1,406.6	1,124.1
Copper River Area	780.0	946.0	1,131.1	568.2	797.2
Southeastern Alaska	923.9	1,085.3	1,054.1	971.5	830.8
Washington & Oregon	556.7	1,050.9	1,403.3	2,193.6	947.7

Source of data: International North Pacific Fisheries Commission, 1964-68, and from Supplemental data provided to the INPFC by the USSR.

DEVELOPMENT AND EARLY LIFE HISTORY OF THE NORTHERN SENNET, *Sphyraena borealis* DeKAY (PISCES: SPHYRAENIDAE) REARED IN THE LABORATORY[1, 2]

EDWARD D. HOUDE[3]

ABSTRACT

Eggs and larvae of the northern sennet, *Sphyraena borealis* DeKay, are described from laboratory-reared specimens. Fertilized eggs were collected on the edge of the Florida Current near Miami in December 1969. Larvae were 2.6 mm SL (standard length) at hatching and 13.5 mm SL at 21 days after hatching. Head and snout length increased rapidly relative to standard length as larvae grew. A fleshy tip developed on the lower jaw when larvae were longer than 5 mm SL. Teeth also first appeared at about 5 mm SL. Myomere and vertebral numbers were constant at 24. Ossification of the axial skeleton began in the cephalic region and proceeded caudad as growth occurred. Fin ray complements were complete at about 13.5 mm SL. Pigmentation during development is described and illustrated. Behavior of laboratory-reared *S. borealis* larvae is discussed. Several wild-caught post-larvae were used to extend the descriptive series and helped to validate the identification of the laboratory-reared larvae.

Little is known about early development of barracudas (Sphyraenidae) in the Western Atlantic Ocean. Larvae of the northern sennet (also called northern barracuda), *Sphyraena borealis* DeKay, recently were reared in the laboratory, and the eggs, yolk-sac larvae, and early post-larval stages are described in this report from a series of preserved specimens, providing the first description of this species in its earliest life stages. De Sylva (1963) described some post-larval *S. borealis* and presented keys to identify the postlarvae of western North Atlantic sphyraenids longer than 5.5 mm SL (standard length).

Some confusion exists regarding the systematic relation of *S. borealis* and the similar *S. picudilla* Poey (southern sennet). The two species are regarded by de Sylva (personal communication) as valid species, separable on minor morphometric characters in adults. Briggs (1958) reported *S. borealis* to be distributed nearshore from Bermuda and Massachusetts to Panama, including the north central Gulf of Mexico. Adults of *S. borealis* from southern Florida intergrade in many characters toward those of *S. picudilla* (de Sylva, personal communication). Postlarvae reared in the laboratory during this study always closely resembled the *S. borealis* described by de Sylva (1963).

The eggs and yolk-sac larvae of *Sphyraena argentea* Girard from the eastern Pacific were described by Barnhart (1927). Orton (1955) also described *S. argentea* eggs and yolk-sac larvae as well as older larvae of about 4 and 7 mm TL (total length). Eggs and young larvae of *S. pinguis* Günther from the western Pacific were described by Shojima, Fujita, and Uchida (1957), and their development was reviewed by Uchida et al. (1958). Development of *S. sphyraena* Linnaeus collected in the Mediterranean was summarized by Vialli (1956), and illustrations of some stages were presented by Lo Bianco (1956). Development of *S. barracuda* (Walbaum), commencing with postlarval stages, was discussed by de Sylva (1963). Except for the material on *S. sphyraena*, complete developmental series appear to be lacking for barracudas. My specimens of *S. borealis* provide a

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complete series of egg and larval development of this species. In addition to the reared specimens, some postlarvae and juveniles of *S. borealis* were collected in nets, helping to extend the series beyond the lengths of the longest specimens reared in the laboratory.

MATERIALS AND METHODS

REARING TECHNIQUES

Pelagic eggs of *S. borealis* were collected in a 1-m, 505-μ mesh plankton net at the sea surface in the Florida Current, about 8 km east of Miami Beach on December 11, 1969, at 10:00 AM EST. Surface temperature was 23.6° C at time of collection. A total of 78 eggs were isolated from the catch. They were incubated and the larvae reared in a 55-liter aquarium. Temperature ranged from 23.2° to 24.5° C and salinity from 33.0 to 34.6‰ during the experiment. Larvae were fed zooplankton collected from Biscayne Bay and nauplii of brine shrimp (*Artemia salina*). Some pelagic fish eggs were added to the rearing tank beginning the 7th day after hatching to provide newly hatched fish larvae as a food source for the sennets. Constant illumination was provided to allow the larvae to feed continuously, both by day and night. Many details of methods used to rear fish larvae were described by Houde and Palko (1970).

PRESERVATION OF LARVAE

Only a small series of eggs and larvae were obtained during development because of the small number (78) of eggs available. Two eggs and 18 larvae were preserved in 5% buffered Formalin during the 23 days of the rearing experiment.

WILD-CAUGHT POSTLARVAE AND JUVENILES

Plankton collections in the Florida Current near Miami Beach between January 13 and January 27, 1970, provided 10 postlarval and young juvenile specimens of *S. borealis* from 7.4 to 30.6 mm SL. In addition, two juveniles, 59.6 and 62.9 mm SL, were collected from Biscayne Bay in a 20-ft beach seine in January 1970. These wild-caught specimens provided data to extend the descriptive series and helped to validate the identification of the laboratory-reared larvae as *S. borealis*.

MERISTICS AND MORPHOMETRICS

Fin rays and spines were enumerated for each of the fins. Myomeres (preanal plus postanal) were counted on each larva when they could be distinguished.

The following measurements were made:

Total length (TL): tip of snout to tip of caudal fin.

Standard length (SL): tip of snout to tip of notochord or, in more developed larvae, to base of caudal rays.

Body depth: height of body, exclusive of finfold, at base of pectoral fin.

Head length: tip of snout to posterior margin of otic capsules in yolk-sac larvae and tip of snout to opercular margin in postlarvae.

Snout length: tip of snout to anterior margin of the fleshy orbit.

Preanal length: tip of snout along midline to vertical from anus.

Eye diameter: horizontal distance from anterior to posterior margin of the fleshy orbit.

Tip of lower jaw: length of fleshy extension on tip of lower jaw.

1st predorsal length: tip of snout to anterior insertion of spinous dorsal fin, measured along the body midline.

2nd predorsal length: tip of snout to anterior insertion of second dorsal fin, measured along the body midline.

All counts and measurements were made using a binocular dissecting microscope and ocular micrometer.

OSTEOLOGY

Six larvae, 7.4 to 17.0 mm SL, were cleared with trypsin and stained with alizarin (Taylor, 1967) to determine the sequence of ossification and to accurately assess the lengths at which fin

rays first develop. A complete study of osteology was not undertaken, but development of teeth and caudal skeleton were examined in detail.

DEVELOPMENT

EMBRYO

Two preserved eggs of *S. borealis* were 1.22 and 1.24 mm diameter. They had single, clear yellow oil globules 0.27 and 0.29 mm diameter. The perivitelline space was narrow and the transparent yolk was vaguely segmented. In eggs that I preserved about 2 hr after collection, the embryo was not well developed and no pigment was visible (Figure 1A). Later stage embryos developed both melanophores and xanthophores on the body, giving the living embryo a greenish appearance to the naked eye. The eggs hatched about 20 hr after collection at an incubation temperature of 24° C.

MORPHOLOGY OF LARVAE AND JUVENILES

Larvae of *S. borealis* were 2.6 mm SL at hatching and were robust due to the large yolk sac (Figure 1B) but became characteristically slender after its absorption (Figures 2 and 3). Body depth averaged 12% SL for larvae from immediately after yolk absorption to juveniles of 21.0 mm SL. Gut length was moderately long in *S. borealis* larvae. Jaws were not elongated on newly hatched larvae but became so shortly after the yolk sac was absorbed and mouth parts became functional. Growth in length of laboratory-reared larvae is given in Figure 4.

Yolk Absorption

The yolk sac was large and nearly spherical at hatching, with its oil globule at the anterior end (Figure 1B). Some yolk and the oil globule remained up to 4 days after hatching (Figures 2A and 2B). Feeding began shortly before the yolk was completely absorbed.

Head Length

The head of recently hatched *S. borealis* was short (Figures 1 and 2), but increased rapidly in length as larvae developed. Head length increased relative to body length from 13% SL for newly hatched larvae to a constant value of about 33% SL for larvae 9 mm SL and longer (Table 1). Over half the head length increase was related to an increase in length of the snout during development.

Snout Length

Snout length increased on developing larvae from about 3% SL 1 day after hatching to a value of about 12% SL at 9 mm and gradually to 14% SL for juveniles (Table 1).

Tip of Lower Jaw

A fleshy tip began to develop on the lower jaw at about 5.0 mm SL (Table 1). Its relative length increased from less than 1% SL to about 3% SL when larvae had grown to 14.5 mm SL (Figures 2 and 3). The structure ranged from 3 to 6% SL on 17 to 30 mm SL wild-caught specimens. On two juveniles, 59.6 and 62.9 mm SL, the length of the fleshy tip was only 3% SL. The length of this structure on both laboratory-reared and wild-caught specimens varied rather markedly.

Jaws and Teeth

The mouth was not developed until larvae were 4.0 mm SL, about 3 days after hatching (Figure 2B). Teeth first appeared on the premaxillary bones at 5.3 mm SL when the jaws became barracuda-like (Figures 2C and 2D). Initially, the teeth appeared bluntly conical but became caninelike when larvae grew to 7.0 mm SL. Teeth were developed on the lower jaw and were developing on the palatine bones at 7.4 mm SL. The palatine bones on larvae longer than 12 mm SL bore the largest teeth, except for the second and third pairs of premaxillary teeth; these were long and directed posteriorly. All

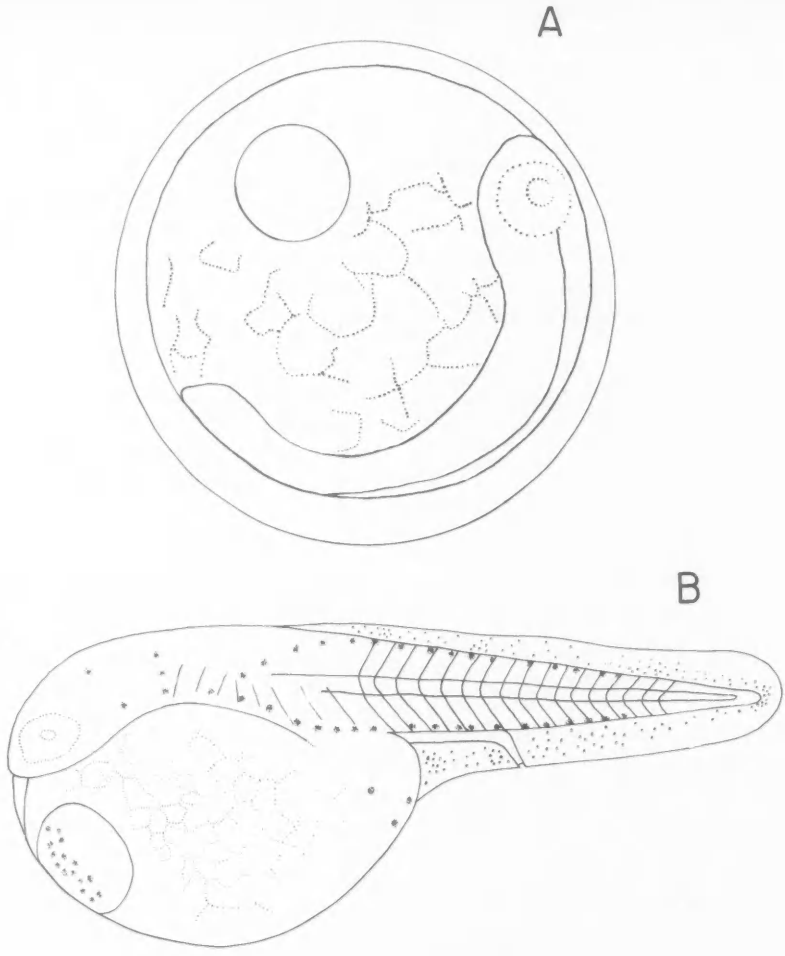

FIGURE 1.—Embryo and newly hatched larva of *Sphyraena borealis*. A. Embryo; B. Newly hatched larva, 2.6 mm SL. Inclusions in the finfold are not pigment.

teeth were strong and caninelike; most were slightly curved and directed backward at their tips. The number of premaxillary teeth increased from 4 at 5.3 mm SL to about 20 at 21.5 mm SL. Lower jaw teeth increased from 11 at 9.4 mm SL to about 15 on specimens from 12.1 to 21.5 mm SL. Palatine teeth numbered 6 at 9.4 mm SL and increased to about 10 at 21.5 mm SL.

Eye Diameter

Eye diameter decreased slightly, from 8% SL on newly hatched larvae to 7% SL for most individuals longer than 16.9 mm SL (Table 1).

Myomeres

The number of myomeres was constant at 24 (14 preanal plus 10 postanal) throughout development.

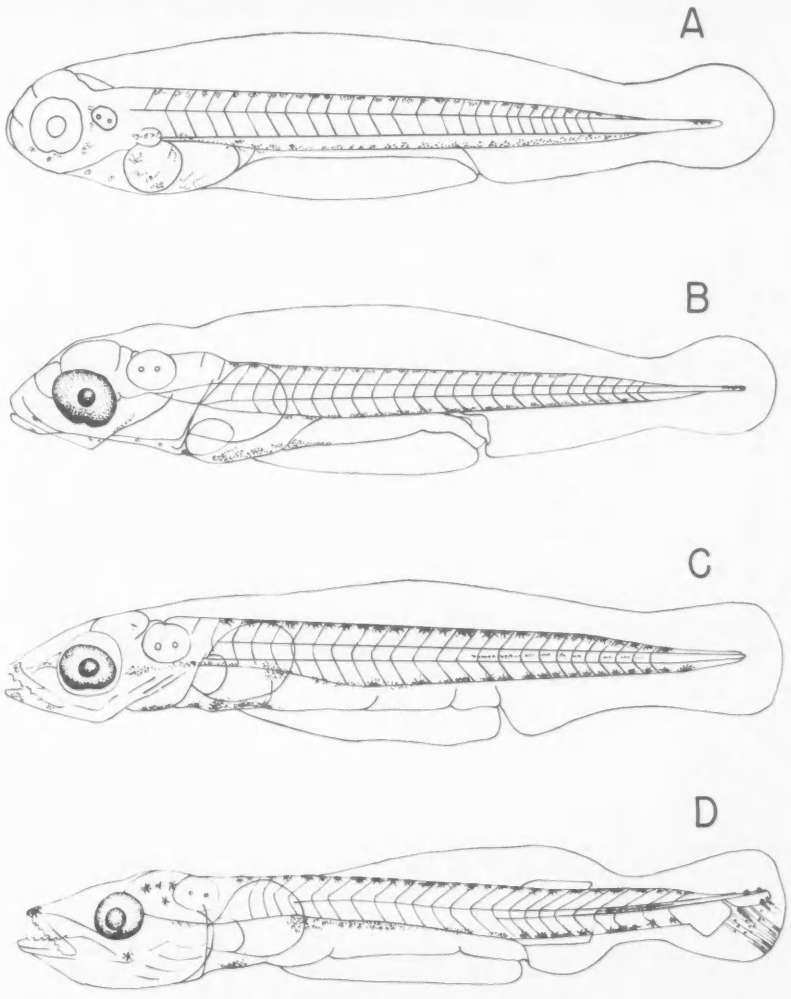

FIGURE 2.—Developmental stages of *Sphyraena borealis* reared in the laboratory. A. 3.8 mm SL; B. 4.3 mm SL; C. 5.3 mm SL; D. 7.4 mm SL.

Keeled Scales

Keeled scales appeared along the lateral line on the caudal peduncle when specimens were about 14.5 mm SL (Figure 3C).

Osteology

Ossification of the axial skeleton proceeded from the cephalic region caudad as growth occurred. A 7.4-mm SL specimen appeared to have nearly complete skeletal development of the head region, but little development posteriorly. Vertebral development was restricted to incomplete neural and haemal arches in the 7.4-mm SL larva. Centra were forming in a 9.1-mm SL larva and appeared to be completely developed

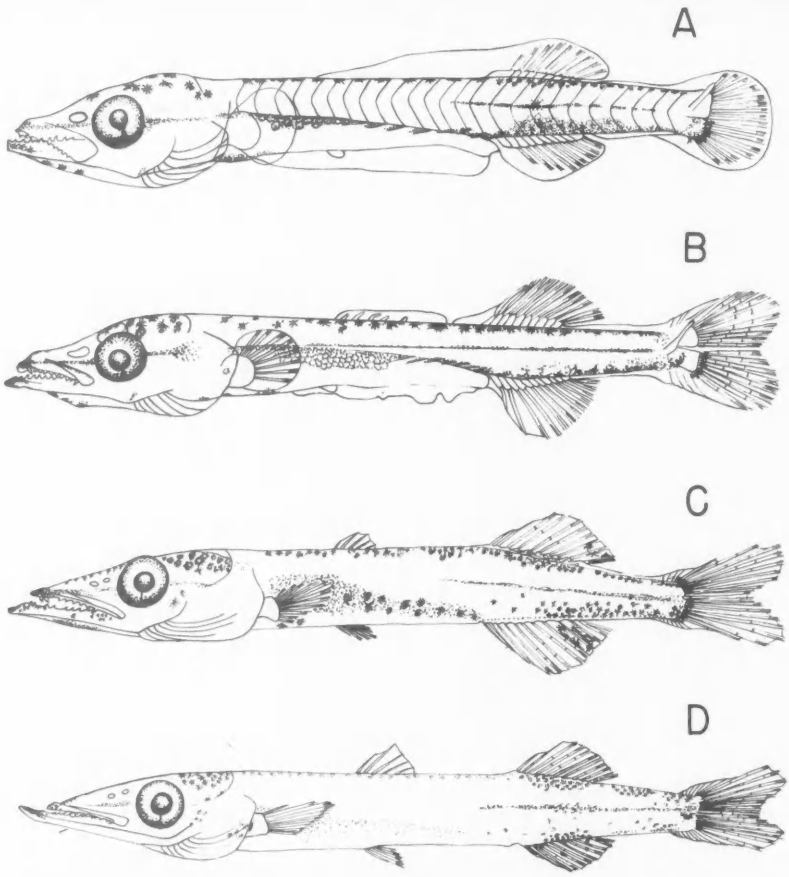

FIGURE 3.—Developmental stages of *Sphyraena borealis*. Specimens A, B, and C were laboratory reared; specimen D was collected in a plankton net. A. 9.4 mm SL; B. 12.3 mm SL; C. 14.5 mm SL; D. 21.0 mm SL.

in a 10.9-mm SL larva. All specimens had 24 vertebrae.

Six branchiostegals were present on the 7.4-mm SL larva and a seventh had developed on the 9.1-mm SL specimen. Cleithra were present but poorly ossified at 7.4 SL; they were well developed at 9.1 mm SL.

Ossification of the caudal region began at 7.4-mm SL. At this size, the hypural bones were developing and some rays could be distinguished in the ventral half of the caudal finfold. All caudal elements were beginning to develop by 10.9 mm SL and were easily recognized on a 12.1-mm SL specimen. The last three vertebrae (including the urostyle) contributed to support of the caudal fin; both neural and haemal spines of the antepenultimate vertebra (22nd) supported developing accessory rays of the caudal fin, as did the haemal spine of the penultimate (23rd) vertebra. A total of 6 hypural bones

TABLE 1.—Summary of morphometric data from laboratory-reared (L) larvae and from wild-caught (W) larvae and juveniles of *Sphyraena borealis*. (Specimens between broken lines are undergoing notochord flexion.) Except for total and standard lengths, measurements are proportional values, the ratio of the character relative to standard length.

Specimen No.	Total length	Standard length	Preanal length	1st predorsal length	2nd predorsal length	Head length	Snout length	Tip lower jaw	Eye diameter
	mm	mm							
3 (L)	2.6	2.6	0.68	--	--	0.13	--	--	--
4 (L)	4.0	3.8	.66	--	--	.14	0.03	--	0.08
5 (L)	4.2	4.1	.63	--	--	.19	.04	--	.08
7 (L)	4.3	4.2	.56	--	--	.19	.04	--	.08
6 (L)	4.5	4.3	.66	--	--	.21	.05	--	.08
9 (L)	5.2	5.0	.65	--	--	.26	.07	<0.01	.08
10 (L)	5.5	5.3	.67	--	--	.26	.07	<.01	.08
8 (L)	5.8	5.6	.68	--	--	.27	.08	<.01	.07
11 (L)	7.7	7.4	.66	--	--	.28	.10	<.01	.07
27 (W)	7.9	7.4	.71	--	--	.30	.12	.02	.08
12 (L)	9.5	9.0	.69	--	0.67	.31	.12	.01	.08
13 (L)	10.2	9.4	.70	--	.68	.32	.13	<.01	.09
14 (L)	12.2	10.9	.70	--	.68	.33	.14	.02	.08
17 (L)	12.9	11.3	.71	0.50	.70	.36	.12	--	.08
15 (L)	13.4	11.9	.69	--	.68	.31	.13	.02	.08
18 (L)	13.7	12.1	.69	.44	.68	.33	.12	.01	.08
16 (L)	13.7	12.3	.66	.44	.66	.32	.13	.03	.08
19 (L)	14.7	12.7	.68	.47	.70	.34	.13	.02	.08
24 (W)	15.9	13.7	.72	.49	.71	.32	.12	.05	.07
23 (W)	16.5	14.4	.72	.48	.70	.36	.15	.04	.08
20 (L)	16.7	14.5	.63	.47	.71	.35	.14	.03	.08
28 (W)	19.4	16.9	.70	.47	.70	.33	.14	.04	.07
26 (W)	19.1	17.0	.69	.48	.70	.32	.14	.04	.06
30 (W)	19.7	17.1	.70	.46	.70	.32	.13	.04	.06
29 (W)	21.2	18.4	.70	.47	.70	.33	.14	.05	.07
21 (W)	24.2	21.0	.71	.49	.72	.34	.15	.06	.08
25 (W)	24.6	21.5	.70	.46	.69	.32	.14	.03	.07
22 (W)	33.9	30.6	.70	.46	.70	.32	.14	.06	.07
32 (W)	66.8	59.6	.71	.46	.70	.32	.14	.03	.06
31 (W)	70.0	62.9	.72	.45	.71	.32	.14	.03	.06

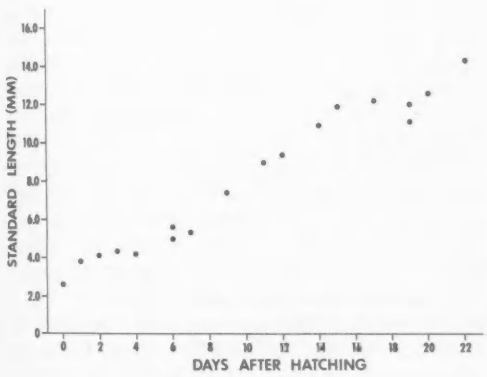

FIGURE 4.—Growth of *Sphyraena borealis* larvae reared in the laboratory at an average temperature of 24.0° C.

were formed near the posteroventral surface of the urostylar vertebra. There were 3 epurals and 2 pairs of uroneurals ossifying dorsal to the urostyle. The 17 principal caudal rays were supported by the hypural bones. Principal caudal ray support was as follows: hypural 1 supported rays 1 to 3; hypural 2 supported rays 4 to 7; hypural 3 supported ray 8; hypural 4 supported rays 9 to 11; hypural 5 supported rays 12 to 15; hypural 6 supported rays 16 and 17. A 17.0-mm SL specimen differed from smaller specimens only in having the first principal caudal ray partially supported by the haemal spine of the penultimate vertebra as well as the first hypural bone. All elements were at least partially ossified at 17.0 mm SL; both the epurals and uroneurals were the most poorly ossified bones of the caudal skeleton at this stage. Hollister (1937) examined caudal skeletons of adult and

TABLE 2.—Summary of meristic data (spines and rays) from laboratory-reared (L) and wild-caught (W) larvae of *Sphyraena borealis*. (Dashes indicate elements were present but could not be accurately counted.)

Specimen No.	Standard length	Principal Caudal rays	Anal fin	2nd dorsal fin	1st dorsal fin	Pelvic fin		Pectoral fin	
						Left	Right	Left	Right
	mm								
3 (L)	2.6	0	0	0	0	0	0	0	0
4 (L)	3.8	0	0	0	0	0	0	0	0
5 (L)	4.1	0	0	0	0	0	0	0	0
7 (L)	4.2	0	0	0	0	0	0	0	0
6 (L)	4.3	0	0	0	0	0	0	0	0
9 (L)	5.0	0	0	0	0	0	0	0	0
10 (L)	5.3	0	0	0	0	0	0	0	0
8 (L)	5.6	0	0	0	0	0	0	0	0
27 (W)	7.4	0	0	0	0	0	0	0	0
11 (L)	7.4	7	0	0	0	0	0	0	0
12 (L)	9.0	16	8	8	0	0	0	0	0
13 (L)	9.4	16	9	9	0	0	0	0	0
14 (L)	10.9	17	10	10	3	0	0	0	0
17 (L)	11.3	17	11	10	5	5	--	8	6
15 (L)	11.9	17	11	10	3	--	--	--	--
18 (L)	12.1	17	11	10	5	--	--	8	8
16 (L)	12.3	17	11	10	4	5	--	8	6
19 (L)	12.7	17	10	10	5	--	--	10	--
24 (W)	13.7	16	11	10	--	5	--	12	12
23 (W)	14.4	17	--	10	5	5	6	--	12
20 (L)	14.5	17	11	10	5	--	6	12	10
28 (W)	16.9	17	11	10	--	--	--	--	--
26 (W)	17.0	17	11	10	5	6	6	11	12
30 (W)	17.1	17	10	10	5	--	--	--	--
29 (W)	18.4	17	11	10	--	--	--	--	--
21 (W)	21.0	17	11	10	--	--	--	--	--
25 (W)	21.5	16	11	10	5	6	6	12	12
22 (W)	30.6	17	11	10	5	6	6	12	12

juvenile *S. borealis*, *S. picudilla*, and *S. barracuda*. She found that all were similar and showed that a progressive fusion of caudal elements occurred in barracudas as they grew. Fusion of hypurals 2 and 3, 4 and 5, and of the urostyle with hypural bones was apparent in her large specimens.

Fin Development

Newly hatched larvae had a prominent larval finfold (Figures 1 and 2) that appeared granular because of many bubbles or small inclusions distributed throughout. These inclusions were not illustrated, except in the newly hatched larva (Figure 1B), but were present until larvae grew to about 9.5 mm SL.

Fin ray development essentially was completed at 13.5 mm SL (Table 2). Fan-shaped pectoral fins without rays developed at 3.8 mm SL 1 day after hatching (Figure 2A). Rayed fins developed in the following sequence: caudal, anal and second dorsal, first dorsal, pelvics, and pectorals. The caudal fin rays began to develop at 7.4 mm SL when the notochord started to flex (Figure 2D). All 17 principal caudal rays were present on a 10.9-mm SL larva. Accessory caudal rays (rayletts) also were developing at 10.9 mm SL. Their number varied from 6 to 8 dorsally and 6 to 9 ventrally on specimens up to 30.6 mm SL. The anal and second dorsal fins were represented only by opaque areas in the finfold at 7.4 mm SL, but rays of these fins were developing at 9.0 mm SL; posteriormost rays developed before the more anterior rays and 9 rays were present in each fin at 9.4 mm SL (Figure 3A). A full complement of 2nd dorsal (I, 9) and anal (I, 9 or 10) elements was present at 10.9 mm SL. Spines of the first dorsal fin appeared at 10.9 mm SL and a full complement of 5, located over vertebrae 5 to 7, was present on a 12.1-mm SL larva. The 5 spines were more heavily ossified and located over vertebrae 6 to 8 on a 17.0-mm SL specimen. Pelvic fin buds formed on larvae as small as 9.4 mm SL, but rays did not begin to develop until 11.3 mm SL. Pectoral fin rays also began to develop at this length. All pelvic (I, 5) and pectoral (12) elements were not present on

all larvae until about 13.5 mm SL. Remnants of the larval finfold persisted until 12.5 mm SL (Figure 3B).

Pigmentation

Except where specifically mentioned, references to pigment are to melanophores. Xanthophores were common on larvae, and both silver iridophores and blue chromatophores were present. (See Fujii, 1969, for chromatophore terminology.) Some variations in melanophore patterns were present among *S. borealis* larvae of similar size but the following description gives the typical sequence of development.

Melanophores and xanthophores were present on newly hatched larvae but the latter faded after preservation. Small melanophores were distributed in a dorso-lateral and ventro-lateral row on each side of the larva (Figure 1B). The two rows converged just above the yolk sac and ran anterior as a single row to the posterior cephalic region, joining a series of melanophores located over the hindbrain. Other melanophores were present on the anterior half of the oil globule and near the posterior of the yolk sac.

One to two days after hatching (about 3.8 mm SL), melanophores became larger and more numerous (Figure 2A). Those located in the lateral rows and on the cephalic region became stellate. They were more numerous on the yolk sac and two small melanophores appeared near the developing mouth. A series of two to six small, contracted melanophores were noted near the tip of the notochord. The eye became pigmented at 2 days after hatching.

As larvae developed, both melanophores and xanthophores became more numerous. Xanthophores were distributed over much of the body and consisted of elongate yellow cells forming a loose network on the body. In life, larvae appeared green because of the presence of both yellow and black pigments. Blue iridophores on the hindgut and some iridescent pigment in the eyes also were present.

By 7 days after hatching (about 5.3 mm SL, Figure 2C) stellate melanophores had appeared over the brain, on the tip of the upper jaw, lower jaw, angle of the jaw, ventral margin of the opercular region and over the foregut. Each dorso-lateral row of stellate melanophores was well developed while the ventro-lateral rows were condensing into a single ventro-medial row, posterior to the anus. A mid-lateral series of melanophores was developing posterior to the anus.

At 9 days after hatching (about 7.4 mm SL) pigmentation became more intense (Figure 2D). About 5 melanophores were present in the developing caudal fin. The fleshy tip of the lower jaw began to become darkly pigmented on some specimens at this stage. The extent and intensity of pigmentation continued to increase on older larvae (Figures 3A and 3B). No changes in pattern were observed, except for development of a line of pigment that bisected the eye, and a migration of melanophores from the tip of the developing urostyle to the ventral margin of the hypural plate.

When specimens were 20 to 22 days old (about 12.5 to 14.5 mm SL), the juvenile pattern of dorsal and lateral blocks of pigment began to appear (Figure 3C). Stellate melanophores also developed in the second dorsal and anal fins of individuals of this size. Longer specimens from plankton collections had the typical juvenile pigment pattern (Figure 3C) (cf. de Sylva, 1963; Figure 4).

GROWTH AND MORTALITY

Larvae of *S. borealis* grew most rapidly during the first 14 days after hatching, but more slowly during the next 7 days (Figure 4). Larvae were 2.6 mm SL at hatching, averaged 5.5 mm SL at 7 days after hatching, 11 mm at 14 days, and about 13.5 mm at 21 days. The decrease in growth rate of the sennets during the third week may have been caused by the scarcity of fish larvae in their diet. Average growth rate during the rearing experiment was about 0.5 mm per day.

A total of 78 sennet eggs were incubated but only about 50% hatched. From this small number of hatched larvae, 9 survived until 14 days after hatching, when they had developed most of the characters of juvenile sennets. Mortality in the first 14 days included 11 larvae preserved

for describing larval development. No larvae survived beyond 22 days after hatching, probably because of the inadequate diet.

TRANSFORMATION

Transformation from the larval to the early juvenile stage occurred at about 13.5 mm SL for *S. borealis*. At that size, fin ray development was complete and there were no remnants of the larval finfold. Additional evidence that this size marked the end of the larval period was the occurrence of keeled scales on specimens at 14.5 mm SL and the appearance of juvenile pigment patterns between 12.5 and 14.5 mm SL.

COMPARISONS

Among the four early life history series of barracudas that have been described in the literature, newly hatched larvae of *S. borealis* most closely resemble those of *S. pinguis* from Japanese waters (Shojima et al., 1957; Uchida et al., 1958), except for size at hatching. In both species, the oil globule, at hatching, is located at the anterior end of the yolk mass; neither develop melanophores in the finfold. In contrast, the oil globule is located at the posterior end of the yolk mass in newly hatched larvae of *S. sphyraena* (Vialli, 1956) and *S. argentea* (Orton, 1955) and both have melanophores in the finfold.

Eggs of *S. pinguis* (0.69 to 0.82 mm diameter) were considerably smaller than those of *S. sphyraena* (1.11 to 1.15 mm), *S. borealis* (1.22 to 1.24 mm), and *S. argentea* (about 1.5 mm). It is not surprising that at hatching, larvae of *S. pinguis* were smaller than those of *S. borealis*, measuring 1.75 mm as compared to 2.6 mm. Both species were similarly pigmented at hatching, but differed significantly by 45 and 66 hr. Melanophores were larger and more concentrated in *S. pinguis* larvae than in *S. borealis* at the same stage of development.

Older larvae of *S. borealis* and *S. sphyraena* had similar pigment patterns, but those of *S. sphyraena* had a more developed lower jaw tip. Three-day-old larvae of *S. argentea* from California waters had a distinctive band of melanophores on the tail portion of the body just posterior to the anus that was lacking in *S. borealis*. Postlarvae of *S. barracuda* were described and illustrated by de Sylva (1963). They differ substantially from *S. borealis* in being deeper bodied and having a relatively longer snout. Pigmentation of *S. barracuda* and *S. borealis* larvae between 5.5 and 11.9 mm SL also differs somewhat in its detail.

BEHAVIOR

Newly hatched larvae of *S. borealis* drifted about the rearing tank making only occasional feeble swimming attempts when disturbed. At 2 days after hatching, larvae maintained a horizontal position and began swimming actively with short darting motions. Feeding activity was first observed 3 days after hatching. Sennet larvae usually fed using the *S*-flex behavior previously described for many species of clupeiform larvae (e.g., Rosenthal, 1969; Schumann, 1965). Occasionally, however, a sennet larva would strike at a food organism without first flexing its body and examining the item. Zooplankton organisms less than 100 μ in body width were the initial food of larvae. No stomach analyses were carried out on sennet larvae, but most of the food which was placed in the tank were copepod nauplii and copepodites.

Sennet larvae continued to feed on small zooplankton organisms until 10 days after hatching, even though larger plankton, including fish larvae, and nauplii of brine shrimp were present in the tank beginning 7 days after larvae hatched. At 10 days, large plankton (about 300 to 400 μ body width) was accepted as food, as were some unidentified, newly hatched fish larvae about 2 mm in length. A sennet larva would approach a tiny fish larva, assume an *S*-flex position and dart out at the larva, usually seizing it crosswise. Before swallowing it, a sennet would shake the larva and turn it so that its long axis was parallel to the sennet's alimentary tract. Sennets would swallow fish larvae either head or tail first. Fish larvae were the preferred food of sennets longer than 9 mm SL, but this food was not provided in sufficient quantities to satisfy the sennets. Cannibalism was not observed, but sennets became aggressive toward one an-

other at 11 days after hatching. If size variation had been great or if the sennet larvae had been crowded in the rearing tank, cannibalism likely would have occurred.

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SENSORY FACTORS IN THE SIDE-TO-SIDE SPACING AND POSITIONAL ORIENTATION OF THE TUNA, *Euthynnus affinis*, DURING SCHOOLING

PHYLLIS H. CAHN[1]

ABSTRACT

This study was designed to demonstrate the role of the lateral line sensory system in fish schooling. Groups of 2, 3, 4, and 6 adult *Euthynnus affinis* were filmed during schooling orientation in the presence or absence of transparent partitions between them. When the hydrodynamic field between orienting fish was blocked by the partition, they significantly increased their side-to-side spacing, and changed their diagonal to abeam position ratios so that abeam orientation assumed increased importance. Apparently, hydrodynamic contact is essential for the typical spacing and positional orientation in schooling, and the lateral line, as the water turbulence detector, plays a prime regulatory role.

The primary role of vision for the initial approach and prolonged maintenance of parallel orientation of fish in a school has been well known for many years (Parr, 1927). The accessory role of other sensory systems, especially the acoustico-lateralis, for maintenance of fish-to-fish distance during schooling, has been implicated by numerous investigators (Breder, 1959, 1965; Cahn, Shaw, and Atz, 1968; and Moulton, 1960), but direct evidence has been difficult to obtain. Breder (1965) showed that the side-to-side spacing of danios in a school (*Brachydanio albolineatus*) is "usually just a little over twice the distance from the side of each fish to the outer edge of the trail of vortices" each generates while swimming. He considered that the fish space themselves so as to "respect these vortices or suffer a considerable reduction in locomotor efficiency". Thus, the sensory system primarily involved in hydrodynamic detection should play a key role in regulation of this spacing. Our work (Cahn, Siler, and Fujiya, in press), and that of Dijkgraaf (1963), strongly implicates the lateral line mechanoreceptors in this function.

In a preliminary report on tuna schooling (Cahn, 1967), it was found that a transparent partition that blocked hydrodynamic contact between orienting fish also resulted in somewhat diminished fish-to-fish attraction, and in changed spacing and positional relationships. Prior to this study, many other investigators of fish schooling tried to separate the sensory components involved, and used transparent plastic and glass boxes, tubes and plates, as well as mirrors (reviewed by Shaw, 1970). Variable results were obtained, with little quantification, except for Shaw's study on *Caranx hippos* (1969), which showed a reduced duration of schooling when the fish were separated by transparent partitions.

The present study quantifies the changes in spacing and positional orientation of the tuna, *Euthynnus affinis* (common name, kawakawa), observed in the earlier report, when transparent partitions blocked non-visual schooling cues. The results strengthen the role of hydrodynamic detectors in control of fish positional relationships and side-to-side distance between fish in a school.

MATERIALS AND METHODS

This work was carried out at the Honolulu Biological Laboratory of the National Marine Fisheries Service, where the facilities are available for experimental studies on scombroid fishes. Special transport containers (Nakamura,

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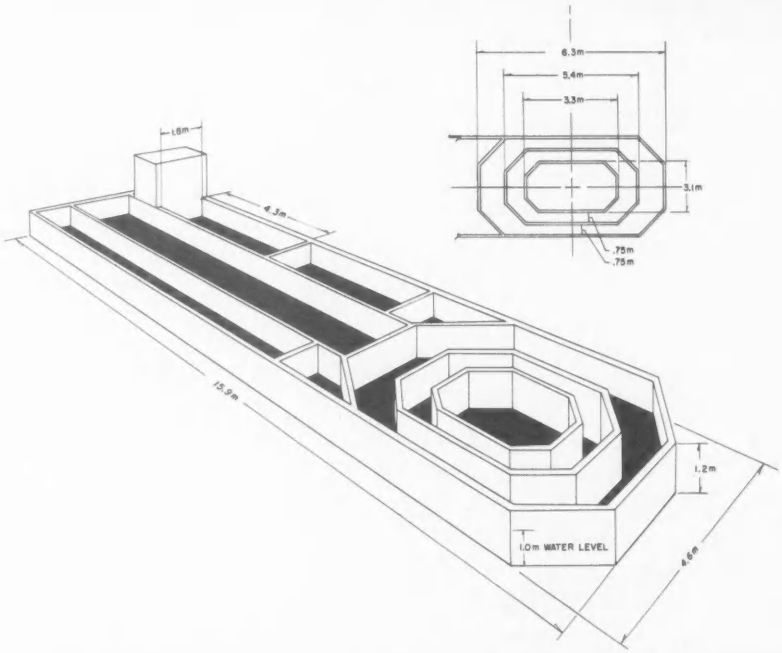

FIGURE 1.—Schematic diagram of cement tank used for tuna schooling studies. Insert shows true dimensions of octagonal channels formed by acetate partitions. Rectangular sidearms were divided in half lengthwise by the Plexiglas partitions, not shown here. Center rectangle was used as a catwalk.

1962) permit the fish to remain in the water from the time of capture until release into tanks on shore.

The experiments were done in a large cement tank that consisted of several differently shaped compartments (Figure 1). An octagonal area at one end was attached by moveable gates (not shown in figure) to rectangular sections at the other end. With the gates up the fish could be transferred to one or the other section without renetting for each experiment. Two concentric octagons of transparent acetate formed three separate swimming compartments for the experimental studies in the octagonal area; in the rectangular areas, rigid, 6.3 mm thick, transparent Plexiglas formed the partitions. The more flexible acetate permitted some hydrodynamic transfer, but the rigid Plexiglas did not. In one series of tests with the Plexiglas partitions, circular holes, 1.25 cm in diameter, were evenly spaced about every 15 cm along the partition.

Films were taken from observation booths at the ends of the sidearms and above the ceiling, over the octagonal area. A 16 mm Bolex was operated at 16 frames per second; a 10 mm Kern-Paillard Switar or a 5.7 mm wide-angle Kinoptic Tegea lens was used. Single frame analysis of selected sequences provided data for quantitative study (L-W Inc. Photo Optical Data Analyzer, Model 224 A, Van Nuys, Calif.). At the film speeds used, it was satisfactory to measure every fifth frame, since positions changed minimally during this time interval. The number of frames given in the tables should

be multiplied by five to reflect the number of frames examined.

Eighteen fish out of 22 adapted to the test conditions; they were tested in groups of 2, 3, 4, and 6, and each fish was used in more than one test. To determine the side-to-side distance between fish that were in parallel orientation, the position of each fish and his body axis were drawn from the motion picture frames. The perpendicular distance between the axes of pairs of orienting fish was measured (Figure 2).

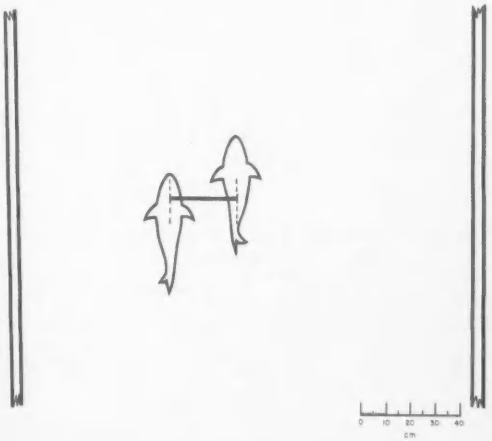

FIGURE 2.—Scale diagram showing tunas swimming without a partition in rectangular channel. The dimensions were taken from a fish of 43 cm fork length. Body axes are shown as dashed lines. The side-to-side distance of 25.9 cm (solid line) is the group mean for a school size of 2 fish.

When occasional non-parallel axes were encountered, the inter-fish spacing was measured from the snout of the leading fish perpendicular to the axis of the trailing fish, or from snout-to-snout if the fish were abeam. The slight body undulations produced while swimming and when each fish turned resulted in slight angular differences in the headings of two otherwise parallel fish. For our purposes it was not necessary to measure these angles, although we spot-checked the first frame of each sequence used to be sure that the angular headings from one another were approximately 26° or less. This was the angular value which Hunter (1968) and Shaw (1969) considered small enough to be counted as parallel fish.

To determine how often two fish in parallel were in an abeam position (directly alongside each other, as in Figure 3), or in a diagonal relationship (alongside, but slightly in front or behind), we scored each frame of the measured sequences as abeam or diagonal, and counted the total number of frames the fish were in these positions. Initially, we measured the diagonal distances to get some idea of how far ahead or behind each other the fish were keeping. At the turns, however, these values became difficult to keep track of. For our purposes, we found it satisfactory to score as diagonal all frames where fish in parallel were more than 5° displaced from a strictly abeam position. We did

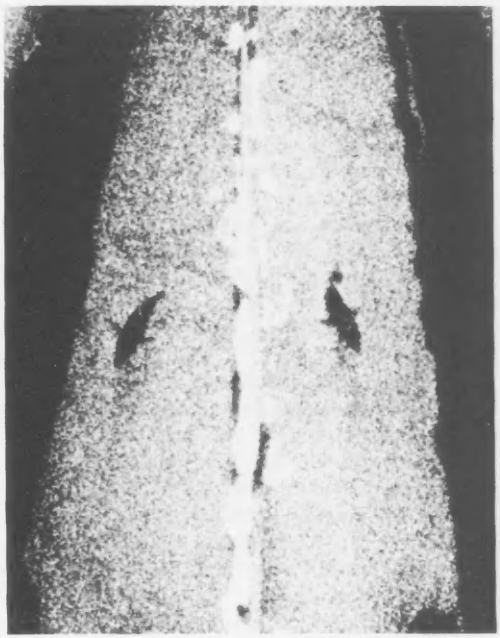

FIGURE 3.—Single frame from test on a pair of fish separated by a Plexiglas partition (top of column in Table 2). Upper edge of partition is obscured by reflection from overhead lights. In this frame the fish are about 93 cm apart, just about the mean distance for this test.

not include any frames where fish were in single file formation.

Kawakawa does especially well in captivity (Magnuson, 1965). Young adults were used, of about 37 cm fork length; they had been in holding tanks with running seawater for about 6 months, and appeared normal in all respects. Thawed marine smelts (California osmerids), were fed daily. The water temperature was 23 to 26° C, and was pumped into the tanks at 520 liters/min from a storage sump fed by a well 6 to 9 m deep. The salinity was 33 to 35‰. Dissolved oxygen levels averaged 6 mg/liter. A 1,000 watt and a 300 watt underwater incandescent light, at the bottom of the tank, were used, in addition to banks of overhead fluorescents, to simulate daylight.

RESULTS

In the absence of partitions the diagonal to abeam position ratios for fish orienting in parallel were 5.17/1 and 6.04/1 respectively in the rectangular and octagonal areas. It appeared that the abeam position was assumed for only brief periods when changing speeds in the course of altering direction, turning, or shifting position in the school. In the presence of partitions the ratios were 1.28/1 and 2.36/1 respectively in the rectangular and octagonal areas. Thus the abeam position assumed increased importance during parallel orientation with partitions (Table 1).

The side-to-side spacing is shown in Table 2 as the mean distance apart of either the two fish in a group of two, or of the two closest fish in a group of three or more. Each mean represents measurements made between a single pair of fish during a single continuous film sequence. Without partitions, this distance ranged from 14.0 to 29.8 cm in the rectangular area, and 13.4 to 23.0 cm in the octagonal area. Fish separated by a partition stayed much farther apart; the side-to-side spacing ranged from 64 to 134 cm in the rectangular area (Figure 3), and from 30 to 82 cm in the octagonal area. Fish-to-partition spacing varied from a minimum of about 7 to 8 cm to a maximum of about 75 cm, and appeared to depend on the location of the other fish (Figure 4). Circular holes in the Plexiglas did not change the spacing (Table 2). Water movement through the holes was very slow. Fifteen minutes after fluorescein dye was placed on one side

TABLE 1.—Positional orientation of schooling *Euthynnus*.

	Test area	School size	Total no. frames analyzed[1]	Positions of parallel fish: No. frames diagonal (*D*)	Positions of parallel fish: No. frames abeam (*A*)	D/A ratio
No partition	Rect.	2	132	110	22	
		3	118	99	19	
		6	96	81	15	
				290	56	5.17/1
	Oct.	2	49	46	3	
		3	44	32	12	
		6	69	61	8	
				139	23	6.04/1
Partition	Rect.	2	360	201	159	
		3	36	25	11	
		4	24	10	14	
				236	184	1.28/1
	Oct.	2	51	36	15	
		3	82	52	30	
		6	52	42	10	
				130	55	2.36/1

[1] These are equal to the number of frames measured for each category in Table 2.

TABLE 2.—Side-to-side spacing of *Euthynnus* in schooling orientation.

Test area	School size	Mean distance apart and standard error: No partition: Dist. (*cm*)	SE	No. frames	Partition: Dist. (*cm*)	SE	No. frames
Rect.	2	22.0	3.4	(25)	92.4	4.2	(121)
		29.8	2.6	(107)	94.0	2.4	(186)[1]
				132	134.0	5.3	(53)
							360
	3	14.0	0.8	(24)	64.0	6.0	(18)
		17.4	1.0	(94)	90.0	4.4	(18)
				118			36
	6	15.2	0.4	(66)	74.0	2.8	(24)[2]
		16.2	2.4	(30)			
				96			
Oct.	2	19.6	0.6	(22)	30.0	2.1	(21)
		23.0	0.4	(27)	82.0	6.0	(30)
				49			51
	3	20.0	3.0	(21)	48.0	2.8	(27)
		20.0	0.6	(23)	49.5	1.3	(55)
				44			82
	6	13.4	1.0	(27)	42.0	2.2	(30)
		14.8	1.0	(42)	56.0	2.6	(22)
				69			52

[1] This partition contained the series of holes.
[2] There were only 4 fish in this group.

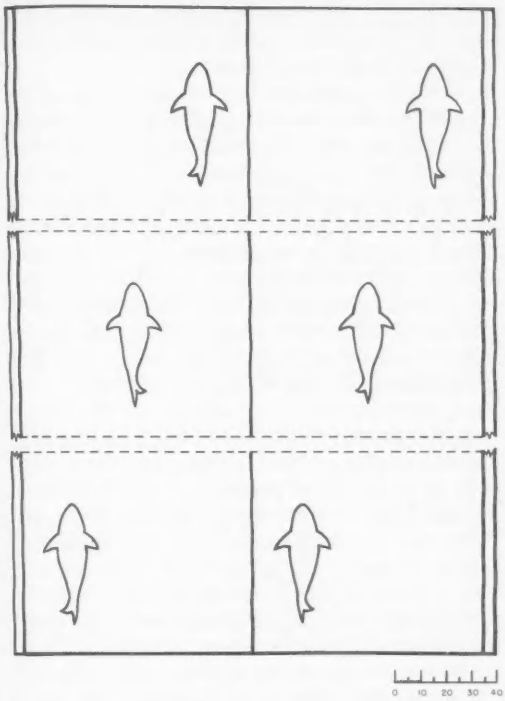

FIGURE 4.—Scale diagrams of tunas swimming with Plexiglas partition in rectangular channel. The 3 usual positions assumed relative to the partition are shown.

the amount that crossed to the other side was barely perceptible.

The data on the side-to-side spacing are summarized in Table 3, where the standard errors were calculated from the variance of the means of the runs in Table 2. It will be noted that in the presence of partitions the variability is much greater. A three-way analysis of variance on the group means (Table 4) showed that the increased spacing in the presence of partitions was highly significant. Although there was a tendency for the fish to remain slightly more compact in the larger groups, these differences were not statistically significant; the effects of shape of the test area was very close to but not quite significant.

TABLE 3.—Summary of data on side-to-side spacing of *Euthynnus* in schooling orientation.

Test area	School size	Group means and standard errors (*cm*)	
		No partition	Partition
Rect.	2	25.9 5.5	106.8 23.3
	3	15.7 2.3	77.0 18.2
	6	15.7 0.7	74.0 —[1]
Oct.	2	21.3 1.8	56.0 36.0
	3	20.0 —[2]	48.7 1.1
	6	14.1 0.9	49.0 9.9

[1] There was only one mean in this case; also only 4 fish in the school.
[2] The two means in this group were the same.

TABLE 4.—Three-way analysis of variance[1] of group means for side-to-side spacing of *Euthynnus*.

Source of variance	Sum of squares	Degrees of freedom	Mean squares	*F* Ratio	Significance level
Total	10,037.42	11			
P or no P	7,440.92	1	7,440.92	44.02	$F_{0.9995}(1,7)=37.0$ $P<0.0005$
Test area	936.94	1	936.94	5.54	$F_{.95}(1,7)=5.59$ not sig.
School size	476.45	2	238.23	1.41	not sig.
Residual	1,183.11	7	169.02		

[1] Fisher, 1970.

Swimming speeds in the absence of partitions ranged from 50 to 64 cm/sec in both rectangular and octagonal areas. With partitions, in the rectangular channels the two orienting fish swam at about the same speed within the range of 50 to 64 cm/sec. During turns, usually made at the ends of the rectangles, they almost always maneuvered to begin the next lap together. Orientation persisted for periods as long as nine days for one pair. In the octagonal area the duration of fish-to-fish orientation was never longer than two days. The size differences between the octagonal channels necessitated differences in swimming speed to maintain fish-to-fish orientation. For example, the fish in the outermost octagon had to swim excessively fast (over 65 cm/sec) to maintain contact with the fish in the innermost section, swimming abnormally slowly (34 cm/sec). Therefore most of the data was obtained in the two larger octagonal channels, where the fish swam at close to normal speeds, at almost 50 to 64 cm/sec.

DISCUSSION

These results demonstrate that blockage of hydrodynamic contact between fish in a school resulted in a significant alteration in side-to-side spacing and a changed ratio of diagonal to abeam positional orientation. Of the various sensory factors of importance in the changes observed, it appears that the loss of acoustico-lateralis cues from neighboring fish played a key role. Some of the alternative explanations are discussed and dismissed below. We did not do any acoustic calibrations; the cement channels and plastic barriers may have caused some resonance of fish swimming sounds, and these may act as orientation cues. But this would assume that the sounds were above the auditory thresholds for these fish, and that the sound can be directionally localized; the latter supposition we can hardly make, as yet, even for other fish whose hearing ability has been extensively studied, with the exception perhaps of goldfish (Moulton and Dixon, 1967). We know nothing about hearing in kawakawa; the yellowfin, *Thunnus albacares*, has moderately good acoustic sensitivity, and also has a swimbladder, an organ that may be helpful for sound pressure to reach the ear (Iversen, 1967). Kawakawa lack a swimbladder; we therefore believe it unlikely that sonic pressure is as important in the lives of these fish as is hydrodynamic particle motion. The latter was blocked by our partitions, so that mate-generated cues to the lateral line mechanoreceptors were obstructed.

There are several hydrodynamic factors to be considered: while it is true that the partitions changed the hydrodynamic field around the fish, and that the solid Plexiglas could possibly cue him to move farther away and thus increase the fish-to-fish spacing, we do not believe this to represent the primary dynamics involved. The increased spacing appeared from our data to represent primarily the fish-to-fish orientation (Figure 4); this orientation resulted in fish moving close to the partition just as often as they moved away from it, while tracking their mates. At all times the fish keep a certain minimal distance of 7 to 8 cm from the barrier, so that we can say that there is some "orientation" to the partition. Superimposed on this is the fish-to-fish orientation, and this exerts the major control of the side-to-side spacing.

Hydrodynamically, when two fish of about the same size are swimming side by side (abeam position) at about the same speed, there would be virtually no centrally located vortices between them. This is because the vortices generated by each fish trail slightly behind him (Rosen, 1959). The flow patterns at the center would, under these conditions, not be very useful as cues. For the fish to get maximal mate-generated hydrodynamic cues it therefore appears that the diagonal positional orientation is preferable. This preference for "diagonal position to each other over positions in front, behind, or directly abeam" was pointed out by Cullen, Shaw, and Baldwin (1965) in their three-dimensional analysis of fish school geometry. Van Olst and Hunter (1970) also called attention to the fact that "the minimum possible lateral space between neighbors to the side would be lower if fish consistently occupied diagonal positions than if they were perfectly aligned, because the areas of tail movement would not overlap." In relationship to our experimental results, the partitions blocked the mate-generated vortices so there was no longer any "advantage" to the diagonal position. The "advantage" factor, it should be emphasized, is not only for hydrodynamic cues from schoolmates, but also more importantly, to derive maximal locomotor efficiency while travelling in a school. The fish can best use the energy from mate-generated vortices if he is positioned within the influence of the vortex, and this is usually best at primarily right angles and a little behind the course of the fish (Breder, 1965), the diagonal position.

Since the fish, in the presence of the partitions, did not completely abandon the diagonal positioning while increasing the abeam orientation, the question comes up of whether or not vision is equally good from both positions? Tuna vision has been studied to a limited extent; for example Nakamura (1968) studied visual acuity in kawakawa by testing the fish's response to various targets. This involved the temporal region of the retina as the fish swam forward towards the target. A different region of the retina is no

doubt involved in lateral vision, with a perhaps different cone distribution. Nakamura did not study this for kawakawa, but others have demonstrated that schooling fish are nearsighted in forward vision but farsighted in lateral vision (Baylor and Shaw, 1962). This suggests that perhaps the kawakawa in our experiments with partitions shifted spacing and position to make more use of lateral vision. A possible reason may be that in the absence of mate-generated hydrodynamic cues, nearsighted vision is inadequate for efficient tracking of their schoolmates. To explain all of these visual factors, more information is needed on such problems as resolution and cone density in the different retinal regions of kawakawa.

One other question relative to vision requires some comment: did the partitions produce reflections sensed by the fish which led to the changes observed? As previously noted, fish in a school in the presence of a partition positioned themselves in different locations relative to the barrier, depending on the fish-to-fish distance across the partition, rather than on the distance from the partition (Figure 4). Thus if there were any reflections, they did not appear to be of any significance. The schooling tendency predominated: relative to this it should be pointed out that it is unlikely that the change in spacing could be attributed, to any major extent, to a waning of the stimulus to school. Fish-to-fish orientation sometimes persisted across the partition for as long as nine days.

We have considered the prime sensory factors, and omitted tactile and chemical contributions. Since these fish rarely touch each other when swimming except under special circumstances of school structure and size (Breder, 1967), there is no need for further concern with the tactile sense. Chemical cues, in our opinion, were probably not transmitted rapidly enough across or through the partitions to be of any consequence. Even with holes in the partitions, as in one series of tests, water-borne transfer was very slow. Also, the part played by chemoreception in fish schooling (McFarland and Moss, 1967; Moss and McFarland, 1970) appears unimportant for obligate schoolers such as tunas and other scombroid forms (the use of obligate here is as in Breder, 1967).

The greater variability noted in the side-to-side spacing in the presence of a partition reflects, in our opinion, what happens when the normal hierarchy of sensory systems is interfered with. The dynamic stability of a fish school depends on feedback from all of the different senses. The partitions disrupted this balance, and although schooling persisted, certain limitations were imposed on the process.

In conclusion, this study suggests that the diagonal fish-to-fish positional orientation and the side-to-side spacing assumed during schooling may be more essential for hydrodynamic detection than for visual cues.

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A PREDATOR-PREY RELATIONSHIP BETWEEN THE LEATHER STAR, *Dermasterias imbricata*, AND THE PURPLE URCHIN, *Strongylocentrotus purpuratus*

RICHARD J. ROSENTHAL[1] AND JAMES R. CHESS[2]

ABSTRACT

During 1969 and 1970, we spent more than 150 hr underwater observing interaction between the leather star, *D. imbricata* and the purple sea urchin, *S. purpuratus*. The majority of the observations were made in shallow (13-15 m) nearshore waters off Pt. Loma, Calif.

The defensive responses exhibited by the purple sea urchin when contacted by the leather star indicated the presence of a well-developed predator-prey relationship. The responses included retraction of sea urchin podia, depression of spines, gaping and erection of globiferous pedicellariae, and usually movement away from the asteroid.

Within the study area off Pt. Loma, 437 feeding leather stars were encountered underwater, and of these, 204 or 47% were eating *S. purpuratus*. In contrast, previously published observations by Mauzey, Birkeland, and Dayton (1968) on the feeding behavior of asteroids off the state of Washington indicated that echinoids were excluded from the diet of *D. imbricata*. We suggest that (1) prey density and availability, (2) search time, (3) taste or gustatory preferences of the sea star, and (4) some form of associative learning by the leather star may be responsible for the variation in the feeding behavior of *D. imbricata* in different areas.

Early laboratory studies by Prouho (1890) and Jennings (1907) described the behavioral responses of sea urchins when encountered by predatory sea stars. More recently, Jensen (1966) recorded the responses of two sea urchin species, *Strongylocentrotus dröbachiensis* and *Psammechinus miliaris*, in the presence of the sea star *Marthasterias glacialis*. Since field observations on the feeding behavior of sublittoral sea stars were rarely made, the laboratory studies only provided the basis for speculation about natural predator-prey interactions between asteroids and echinoids.

Sea urchins might appear to be somewhat immune from predatory attacks by other invertebrate species because they possess such formidable looking armature. However, Mauzey, Birkeland, and Dayton (1968) observed the sea star *Pycnopodia helianthoides* feeding on sea urchins both intertidally and subtidally along the shores of Washington state. Leighton (1971) reported that two species of sea stars, *P. helianthoides* and *Astrometis sertulifera*, feed heavily on juvenile sea urchins. Also, Rosenthal and Chess (1970) identified the leather star, *Dermasterias imbricata* (Grube) as a predator of the purple urchin, *Strongylocentrotus purpuratus* (Stimpson) off San Diego, California.

This paper examines in detail the predator-prey interactions observed between the leather star *D. imbricata* and the purple urchin *S. purpuratus* in both laboratory and field situations. *Dermasterias imbricata* is reported from Prince William Sound, Alaska, to Baja California (Fisher, 1930; Feder, personal communication), while *S. purpuratus* ranges along the Pacific coast of North America from Alaska to Cedros Island, Baja California (Ricketts and Calvin, 1962). Both species occur in intertidal and subtidal situations in cooler temperate climates of the Eastern Pacific; however, south of Santa Barbara, California, the leather star is common only in the sublittoral zone.

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DESCRIPTION OF THE STUDY AREA

The main study site was located approximately 1.5 km offshore from Pt. Loma, California (lat 32°42'N; long 117°16'W). The area is within a stand of giant kelp, *Macrocystis pyrifera*, and the bottom in this vicinity is from 13 m to 15 m deep. The primary observation site encompassed an area about 300 m by 150 m. The sea floor within this area is relatively heterogeneous and is composed primarily of siltstone pavement rocks, rocky outcrops, ledges, and intermittent patches of coarse sand. Vertical relief is generally less than about 2 m. Much of the hard substratum was occupied either by the holdfasts of *M. pyrifera* or by low standing, brown algae such as *Pterygophora californica*, *Cystoseira osmundacea*, and *Laminaria farlowii*.

METHODS

Emphasis was directed towards observing the organisms under natural conditions in the sublittoral zone; however, laboratory observations were used in addition to those made in the field. Experiments in the laboratory were designed to supplement our field observations, since it allowed us to observe behavioral interactions between *D. imbricata* and *S. purpuratus* over a more continuous period of time. The laboratory portion of the study was conducted at the NMFS Fishery-Oceanography Center, La Jolla, California. Experimental animals were maintained from February through April 1970, in fiber glass water tables which contained circulating seawater. Water temperatures in the aquaria varied from 12° to 17°C during the period of observation.

The field studies are the result of approximately 150 hours of underwater observations made while scuba diving from November 1969 through November 1970. All of the leather stars encountered underwater within the perimeter of the study area were included in the feeding behavior observations. In each case we recorded the size (center of the aboral area to the tip of the longest arm) of the leather star, and noted whether or not it was feeding. It was usually necessary to turn the leather star over in order to make the feeding observation and identify the prey. In situations where the prey was ingested whole by the leather star, we forced the food item out of the sea star's mouth by applying pressure to the aboral and oral surfaces as described in Mauzey et al. (1968). Measurements were made with plastic calipers or rules, and the data were recorded underwater on plastic slates.

Estimates of leather star density were determined by swimming belt transects 4 m wide and 25 m long. Initially, these transect lines were placed haphazardly along the bottom, running either perpendicular or parallel to the shoreline. However, we also placed lines in predetermined locations where leather stars were believed to be more abundant. Size distributions and density estimates of the *S. purpuratus*, which inhabited the study area, were determined by removing all of the visible purple urchins from 16 randomly selected m^2 quadrats. The quadrats were chosen randomly along two 50-m transect lines. One of the transect lines followed a siltstone ledge, and the other was placed perpendicular to the shoreline through a dense stand of giant kelp, *M. pyrifera*. After removal from the quadrats the *S. purpuratus* were placed into plastic bags and carried to the surface for measurement and enumeration.

Three methods were used in an attempt to determine the rate of feeding and the time necessary for a leather star to digest a purple urchin:

(1) A wire mesh cage which covered an area of 4 m^2 was placed over a natural population of at least 50 purple urchins, and four leather stars were introduced as predators into the cage.

(2) Leather stars were marked with numbered disc tags which enabled us to identify and observe individuals over extended periods of time. The tags were attached to the aboral surface of the leather star with a loop of monofilament line. The line was passed through the leather star's epidermis and under the calcareous ossicles using a heavy duty needle. All leather stars were tagged at the sea surface and immediately returned to the bottom.

(3) In the laboratory we placed seven leather stars and 76 purple urchins into a 0.915 × 4.27 m (3 ft × 14 ft) fiber glass water table. The water

table contained circulating seawater approximately 0.3 m in depth. Bricks were scattered around the bottom of the tank to provide the urchins additional substratum and cover. The concentration of leather stars to purple urchins was considerably higher than normally found in the field; however, we felt that the increased number of leather stars might increase our chances to observe predation in the laboratory.

FEEDING BEHAVIOR OF *Dermasterias imbricata*

The widespread distribution of *D. imbricata* along the Pacific coast of North America is partially reflected in its feeding behavior. *Dermasterias imbricata* is an active predator that feeds primarily on benthic invertebrates, although it has been observed feeding on algal and detrital material. In areas containing abundant prey, both motile and sessile in habit, the leather star seems to exhibit a "preference" for the sessile forms, in that sessile species are eaten more often than the motile forms. Asteroid feeding behavior experiments by Landenberger (1968) and Mauzey et al. (1968), showed that the sea star *Pisaster ochraceus* exhibited preferences for sedentary mussels to alternative food items offered them. Paine (1969) suggested that few additional prey species are consumed as long as mussels are available to *P. ochraceus*. Landenberger (1968) also found that *Pisaster giganteus* preferred mussels to four gastropod species which were offered to the asteroids as alternative prey. Additional observations by Rosenthal (1971) indicated that, in nature, *P. giganteus* displayed a preference for prey which was either immobilized or sedentary in habit.

Feder (1959) felt that differences in the diet of *P. ochraceus* were largely dependent on changes in prey availability within each intertidal location. A similar situation appears to exist with *D. imbricata*, at least in those regions where feeding observations have been made. Mauzey et al. (1968) found *D. imbricata* to be a major predator of actinians along the rocky outer coast of Washington; yet, in the protected San Juan Islands, its diet was composed primarily of holothurians. At Waddah and Tatoosh Islands off Washington, they observed *D. imbricata* feeding on encrusting sponges, colonial tunicates, hydroids, and calcareous ectoprocts. Other localities indicate still additional diets. Feder (personal communication) observed leather stars with stomachs everted on eel grass, *Zostera marina*, in the intertidal regions of Prince William Sound, Alaska.

Off Pt. Loma, California we have observed *D. imbricata* feeding on *Strongylocentrotus purpuratus* (sea urchin), *Strongylocentrotus franciscanus* (sea urchin), *Astrometis sertulifera* (sea star), *Pisaster giganteus* (sea star), *Tethya aurantia* (sponge), *Leucilla nuttingi* (sponge), *Membranipora membranacea* (bryozoan), *Epiactis prolifera* (sea anemone), *Corynactis californica* (sea anemone), *Astrangia lajollaensis* (coral), *Muricea californica* (gorgonian), *Kelletia kelletii* (gastropod) egg capsules, unidentified sponges, holothurians, and detritus. *Strongylocentrotus purpuratus* made up 47% of the feeding observations; *L. nuttingi*, 13%; *A. sertulifera*, 4%; detritus, 27%; and all other items combined, 9%, out of a total of 437 feeding leather stars (Figure 1). Over a one-year period, 927 *D. imbricata* were examined for food items; however, some of these observations were repetitive in that the same leather star was reexamined on a different day of observation.

Feeding was accomplished by either ingesting the prey whole or by everting the stomach and

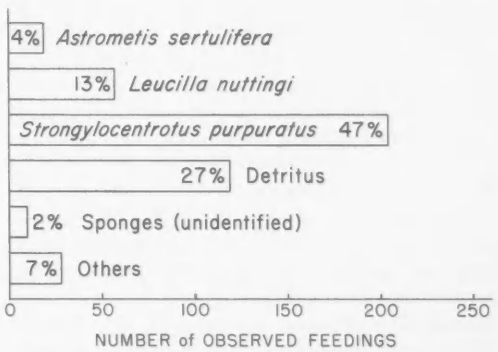

FIGURE 1.—Leather star feeding observations ($N = 437$) off Pt. Loma, California from November, 1969 through November, 1970.

digesting the prey outside of the mouth. Most of the feeding we observed was extraoral in that the leather star's stomach was partially everted out of the mouth (Figure 2). However, the distinction between the two types of asteroid digestion cannot always be determined, since "some species may digest prey partly inside and partly outside the mouth opening at the same time," (Feder and Christensen, 1966, p. 96). In contrast to our observations off Pt. Loma, Mauzey et al. (1968) found that *D. imbricata* usually ingested its prey whole. Again, digestion and method of feeding appears to be dependent on the size and form of the prey species. Often leather stars were observed with their stomachs extended into depressions or everted onto the substrata. In this situation we usually could not identify the food item; however, if the leather star's stomach was everted and there was no prey visible, we assumed that it was feeding on detritus. When feeding observations from the various regions are examined in total, the leather star appears to have a highly variable diet; however, when each location is considered separately the diet becomes much more specialized or restricted.

FIGURE 2.—*Dermasterias imbricata* feeding on a purple urchin 15 m underwater off Pt. Loma. Note the *S. purpuratus* pedicellariae attached to the leather star's epidermis.

PREDATION ON *Strongylocentrotus purpuratus*

Our data indicate that the leather star is a major predator of *S. purpuratus* off Pt. Loma. Of the 437 *D. imbricata* observed feeding, 204 or 47% were preying on *S. purpuratus* (Figure 1). However, this feeding behavior may be an areal phenomenon or even specific to Pt. Loma, since purple urchin predation by leather stars has not been reported from other regions along the Pacific Coast. Mauzey et al. (1968) did not find urchins included in the diets of *D. imbricata* off the coast of Washington, despite the presence of *S. purpuratus*, *S. franciscanus*, and *S. drobachiensis*. All three of these echinoid species appeared to be available to the *D. imbricata* that inhabited these subtidal areas (Dayton, personal communication). One explanation for the exclusion of urchins in the diets of leather stars off Washington might be the availability of alternate or "preferred" prey species. The sedentary or sessile invertebrates which Mauzey et al. (1968) found in the diets of *D. imbricata* off Washington did not appear to be important numerical constituents of the epibenthic community off the Pt. Loma study site. However, the sea urchin population had increased to a point where Leighton, Jones, and North (1966) suggested that perhaps an ecological imbalance had developed within these stands of giant kelp. Further, North and Pearse (1970) reported that an apparent population "explosion" of herbivorous sea urchins had occurred along the coast of Southern California.

In addition to the high percentage of leather stars observed eating purple urchins, we found that 51% of all *D. imbricata* examined off Pt. Loma had *S. purpuratus* globiferous pedicellariae attached to their epidermis (Figures 2 and 3). A laboratory experiment was performed to determine the maximum length of time that globiferous pedicellariae remain attached to the leather star following contact with a purple urchin. We found that following attachment, 3 to 4 days elapsed before the pedicellariae detached from the leather stars. A *D. imbricata* with purple urchin pedicellariae attached to it provided us with indirect evidence that the leather star had either eaten, or had contact with, one or more purple urchins within the last 3 to 4 days. In either case, the number of

FIGURE 3.—Globiferous pedicellariae from *S. purpuratus* attached to the arm of a leather star following contact between the two species in the laboratory.

contacts between the two species off Pt. Loma appears to be quite frequent.

Both species are conspicuous and abundant members of the benthic community within the study area. *Strongylocentrotus purpuratus* was found in densities between 0 and 100 individuals per m^2, with 30.2/m^2 as the mean value within the 16 randomly placed m^2 quadrats. Purple urchin density appeared to vary with the type of substratum. The greatest concentrations of purple urchins were found along or within the siltstone ledges.

We found *D. imbricata* in densities between 0 and 7 individuals per 100 m^2 in the 2,400 sq m of sea floor that was examined quantitatively. Leather stars were most abundant near siltstone ledges and rocky outcrops, where the highest concentrations of purple urchins were also found.

In most instances leather stars were observed feeding on purple urchins which were located in holes or depressions (Figure 4), under ledges, or in the holdfasts of giant kelp. Rarely was urchin predation observed on uniform substratum devoid of irregularities or discontinuities in the bottom. In the field we have observed *S. purpuratus* reacting to the presence of *D. imbricata*. When an approaching leather star disturbed an urchin tactually, it usually evoked a running or escape response. The *S. purpuratus* that inhabited substrata where avoidance maneuvers were possible usually escaped from pursuing leather stars. However, when purple urchins occupied depressions or irregularities along the sea floor, they became more vulnerable to asteroid entrapment and predation.

FIGURE 4.—Leather star feeding on a purple urchin. The sea star has pressed its oral surface into a depression to reach the prey.

In the laboratory most of the purple urchins that were preyed upon were captured on the sides of the water table at the water-air interface. Predation, in this case, appeared to be an artifact of the aquarium, since the two species do not experience this water-air barrier in the sublittoral zone. However, this interface was one of the few physical obstacles besides the corners of the water table that hampered the escape of the purple urchin, and thus allowed a pursuing leather star to capture it. In a similar observation, Mauzey et al. (1968) found that *S.*

purpuratus tended to move to the top of a tank and stop when pursued by *P. helianthoides* in the laboratory.

The 162 *D. imbricata* which were found feeding on whole purple urchins ranged in size (radius) from 79 mm to 166 mm, with 118 mm as the mean value. In comparison, a sample ($N = 344$) of the leather star population within the perimeter of the study area contained individuals from 50 mm to 202 mm and had a mean size value of 108 mm. The purple urchins that were preyed upon ranged from 12 mm to 52 mm in test diameter, with a mean value of 34 mm and a standard deviation of 8.5 mm. For comparative purposes we removed 494 *S. purpuratus* from 16 randomly selected m^2 quadrats. These urchins ranged from 7 mm to 60 mm in diameter and had a mean value of 39 mm and a standard deviation of 8.8 mm. Using these data we compared the mean of the *S. purpuratus* prey and the mean of the urchin population using a *t*-test. We found that at the 5% level there was a significant difference between the two means. It appeared as though the *D. imbricata* were feeding on a smaller size class of *S. purpuratus* than was available to them from the urchin population (Figure 5).

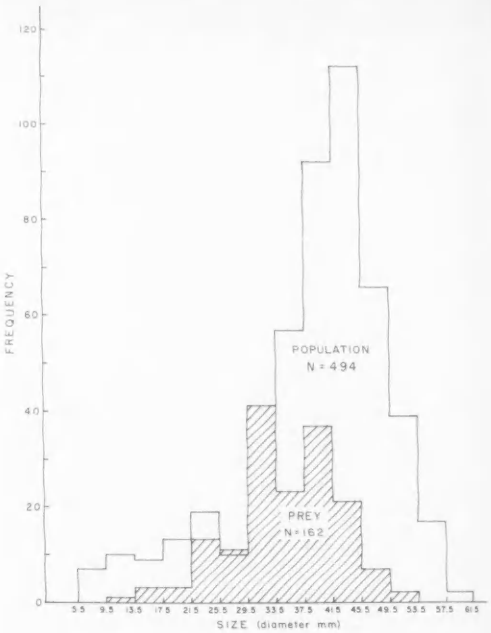

FIGURE 5.—A size frequency histogram comparing the 162 *S. purpuratus* prey with a sample ($N = 494$) from the urchin population within the Pt. Loma study area.

Landenberger (1968) found that in the laboratory large *Pisaster* spp. tended to eat large mussels. To determine if an optimal predator-prey size relationship existed between *D. imbricata* and *S. purpuratus*, the size of each predator and its prey was recorded as a point on a scatter diagram (Figure 6). A non-parametric corner test of association or independence was then applied to these data. We found that the two variables (predator size and prey size) were independent at the 95% level of significance. Therefore, no association between the size of a leather star predator and the size of a purple urchin prey is believed to exist. There was, however, an upper limit to prey size in that we observed no predation on purple urchins greater than 52 mm in test diameter.

FEEDING AND DIGESTION RATES

Most of the purple urchins we observed were killed and digested extraorally by leather stars following capture. However, purple urchins smaller than about 22 mm in test diameter were usually ingested whole. Kjerskog-Agersborg (1918) found that the sea star, *Pycnopodia helianthoides*, digested large prey extraorally, whereas smaller prey were regularly ingested whole.

Determining the feeding rate or number of purple urchins which can be eaten by a leather star over a given period of time was perhaps the most inconclusive aspect of the study. The experiment where leather stars and purple urchins were confined within a 4 m^2 area provided little information on feeding rates in nature. Although three urchins were eaten during the first seven days of observation, we observed no further predation after this initial period. We concluded that the enclosure interfered with the normal movements of the experimental animals, since the four leather stars were fre-

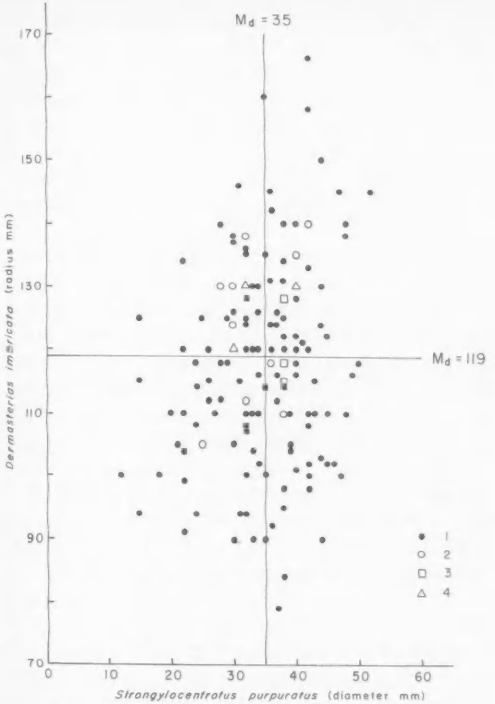

FIGURE 6.—Size of the leather star predator vs the size of the purple urchin prey. Open symbols indicate two or more identical data points.

quently observed crawling on the frame or the wire mesh of the cage.

Our tagging efforts in the field proved to be somewhat more valuable. The disc tags remained attached to the leather stars for at least eight months. During this period we were able to study the feeding behavior of tagged *D. imbricata* on an individual basis. The tagging procedure might have inhibited normal feeding behavior in *D. imbricata*; however, we observed leather stars actively feeding within three days after being marked. Out of 69 marked individuals, the maximum rate of urchin predation occurred with a 151-mm leather star. This individual was observed feeding on three purple urchins (32-36 mm) during seven consecutive days of underwater observations.

Laboratory feeding observations were carried out for 20 days. During this period every one of the seven *D. imbricata* in the water table preyed on at least one *S. purpuratus*. One leather star (140 mm) fed on three purple urchins (16-38 mm) during a five-day period. Sixteen of the 76 *S. purpuratus* present were eaten by the leather stars. The prey ranged from 15 mm to 42 mm in diameter.

From these observations it was learned that the digestion of a purple urchin's soft tissues usually took between 20 and 48 hours. However, on one occasion a 138-mm *D. imbricata* completely digested a 22-mm purple urchin in seven hours. Fisher (1928) reported that *P. helianthoides* digested the soft parts of *Strongylocentrotus* spp. in 24 to 36 hours. The digestion rate varied with the size of the leather star and the size of the prey, as well as the method of digestion. Large purple urchins ($\geq$22 mm), which were usually digested extraorally, were not digested as rapidly as smaller urchins. As an example, 19 hours were required for a 140-mm leather star to digest a 16-mm purple urchin, whereas 28 hours were required for this same leather star to digest a 38-mm purple urchin.

As pointed out in the section on methodology, it was usually necessary to lift up or turn the leather star over to determine whether or not it was feeding on an urchin. In the laboratory, when we disturbed a leather star that had captured or was in the process of digesting a purple urchin, it retracted its stomach, released hold of the urchin, and moved away from the prey. A similar disruption in feeding behavior was also noticed in the field. By marking the *D. imbricata* we had a method which we thought would allow us to study the feeding behavior of individual leather stars in nature. However, the tactile sensitivity that most members of this species displayed negated most of the benefit attained from individual recognition.

One physical factor in nature which appeared to influence predation on *S. purpuratus* by *D. imbricata* was water turbulence. The incidence of urchin predation decreased when a long-period swell generated a strong surge along the bottom off Pt. Loma. For example, on 9 January 1970, we recorded 48% of the *D. imbricata* ob-

served ($N = 60$) to be feeding on *S. purpuratus;* in contrast in this same area on 3 June 1970, only 13% of the leather stars observed ($N = 58$) were eating urchins. On the former day we noted that it was extremely calm underwater, while on the latter a very strong surge prevailed along the bottom at a depth of 15 m. We felt that there was a correlation between water movement and urchin predation by *D. imbricata*, although we had no quantitative measurement of this parameter. Feder (1956 and 1970) found that populations of *P. ochraceus* ate much less in relatively unprotected intertidal areas than in areas which provided the sea stars better protection from wave action.

SPECIES-SPECIFIC REACTIONS

Strongylocentrotus purpuratus reacted to the presence of *D. imbricata* by exhibiting defensive, as well as escape or avoidance, responses. No visible responses were exhibited by *S. purpuratus* which could be considered predator-induced until it was actually touched by a leather star. The podia or tube feet of the purple urchin appeared to be active sites for the reception of chemical and tactile stimuli (Figure 7). In regular urchins, such as *S. purpuratus*, the podia are symmetrically spaced and arranged in five double rows along the sea urchin's test. These podia are capable of extending nearly twice the length of the primary spines and function somewhat like the tentacles or antennae of other marine invertebrates. If viewed from the aboral surface, the area of sensory reception surrounding *S. purpuratus* can best be illustrated by drawing a circle around the urchin, with the locus of the points touching the tips of the fully extended podia.

In the laboratory sea urchin podia were touched with various biotic and abiotic objects to determine which ones elicited avoidance or defensive responses. When touched with human skin, a glass rod, or a "non-predatory" invertebrate, the podia in contact usually retracted and then were extended again. However, if the podia of a purple urchin touched a leather star, the urchin displayed definite signs of predator awareness: in the region of the tactile stimulus, the podia retracted rapidly, spines were depressed, and the poisonous globiferous pedicellariae gaped and became erect (Figure 8). In most instances the urchins moved in the opposite direction of the leather star stimulus.

In another experiment we tested the response of *S. purpuratus* to additional stimuli, using the gaping of the globiferous pedicellariae as an overt sign of predator recognition. The test animals were taken from two populations of *S. purpuratus*. One group was from the jetty in-

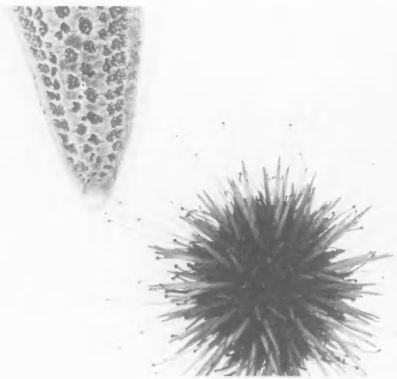

FIGURE 7.—*S. purpuratus* with extended podia just prior to initial contact with the arm of a leather star.

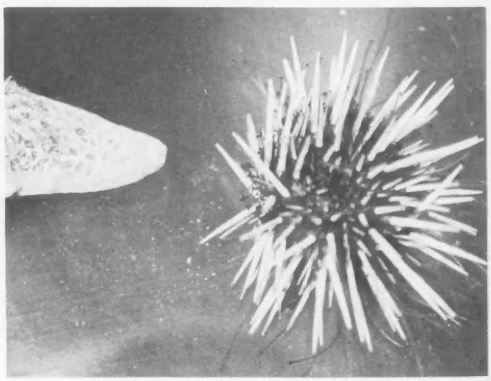

FIGURE 8.—The defensive behavior of *S. purpuratus* immediately after being touched by *D. imbricata*.

side Mission Bay, San Diego County (lat 32° 45′30″ N; long 117°14′30″ W), and the other was from the study site off Pt. Loma. Asteroid tube feet were selected as the biotic stimuli because of the known effectiveness of this tissue in eliciting avoidance reactions in other invertebrate species (Bullock, 1953). Coarse, washed sand grains were used as the abiotic control. Purple urchins were placed individually into glass bowls which contained seawater, and then an asteroid tube foot, or sand grain, was dropped onto the urchin's test. Each urchin was tested for a 2-min period using a different stimulus on each run. Fresh seawater was placed into the bowls prior to each test. The tube feet of *D. imbricata* elicited gaping and erection of purple urchin globiferous pedicellariae in 28 out of 30 test animals. These 28 individuals had an average reaction time of 8 sec, with a range between 2 and 20 sec. None of the *S. purpuratus* displayed gaped globiferous pedicellariae when either *Pisaster giganteus* tube feet or sand grains were presented to them.

Additional asteroids that were found in the sublittoral zone off Pt. Loma were also tested. The tube feet from *Astrometis sertulifera*, *Patiria miniata*, and *Pycnopodia helianthoides* evoked the pedicellariae response in *S. purpuratus;* however, no response was elicited when eight other asteroid species were tested (Table 1). It is interesting to note that the former three species were the only other sea stars, besides *D. imbricata*, that have been observed feeding on live *S. purpuratus* off Pt. Loma.

TABLE 1.—A list of sea stars found off Pt. Loma, California. All 12 species were individually used to test the globiferous pedicellariae response in *S. purpuratus*.

Species	Reaction
Astrometis sertulifera	+
Astropecten armatus	−
Dermasterias imbricata	+
Henricia leviuscula	−
Linckia columbiae	−
Mediaster aequalis	−
Patiria miniata	+
Pisaster brevispinus	−
Pisaster giganteus	−
Pisaster ochraceus	−
Orthasterias koehleri	−
Pycnopodia helianthoides	+

+ = pedicellariae response
− = no pedicellariae response

The erection and gaping of the globiferous pedicellariae initially occurred only on the area of the urchins' test which was directly stimulated by the sea star's tube foot. Jensen (1966) found that a single tube foot from the sea star, *Marthasterias glacialis*, activated the globiferous pedicellariae only in a restricted area on the test of the sea urchin, *Psammechinus miliaris*, whereas the sea star arm tip caused a response from all globiferous pedicellariae. In contrast, we found that the arm tip of *D. imbricata* activated the pedicellariae of *S. purpuratus* only in the region of the stimulus. The defensive response and recognition of predatory stimuli was so acute in *S. purpuratus* that an arm of a *P. giganteus* placed on one side of a purple urchin's test, and a *D. imbricata* arm positioned on the opposite side elicited a response from the globiferous pedicellariae only in the area of leather star contact.

Defensive use of globiferous pedicellariae by sea urchins when disturbed by predatory asteroids has been described by Prouho (1890), Jennings (1907), Jensen (1966), Mauzey et al. (1968), and Rosenthal and Chess (1970). Jensen (1966) reported that the poison contained in globiferous pedicellariae of *Psammechinus miliaris* was not strong enough to paralyze a *M. glacialis*; however, it did have an irritating effect on the sea star which caused it to retreat from the urchin. We found that in some laboratory situations, globiferous pedicellariae bites on the arms of *D. imbricata* caused localized withdrawal of gills or papulae, and a shortening or retraction of the affected arm. Despite this irritation, 90% of all the leather stars we found feeding on purple urchins had from one to over 300 sea urchin pedicellariae attached to their epidermis.

Certain groups of aquatic organisms have been observed to respond to chemical signals or alarm substances emitted by injured conspecifics (von Frisch, 1941; Pfeiffer, 1963; Snyder and Snyder, 1970). Recently, Snyder and Snyder (1970) found that the tropical sea urchin, *Diadema antillarum*, exhibited an alarm or escape response when stimulated with the juices of injured members of its own species. Laboratory and field

tests were conducted to determine if a similar alarm response existed in *S. purpuratus*. A purple urchin within a group of urchins was crushed underwater, and the reactions of neighboring conspecifics noted for 5 min. In both situations we observed no change in movement or alteration in behavior which could be considered alarm oriented following injury to a conspecific. In place of an alarm response we occasionally noted an entirely different reaction from *S. purpuratus* in the laboratory. If a leather star was disturbed while feeding on a purple urchin or moved away from an urchin test following predation, occasionally other *S. purpuratus* in the aquaria approached the conspecific and scavenged the remains.

DISCUSSION

The behavioral responses exhibited by *S. purpuratus* when it is disturbed by *D. imbricata* suggest a well-developed predator-prey relationship. In most instances purple urchins erected globiferous pedicellariae when touched by the four sea stars (*D. imbricata, P. helianthoides, A. sertulifera,* and *P. miniata*) which are known to prey upon them. In contrast, no evasive or defensive responses were noted in the same purple urchins when they were touched by eight additional asteroid species. It appears as though *S. purpuratus* either responds to sea stars that are biochemically similar, or through selection the urchin has acquired the ability to recognize particular asteroid species as potential predators.

The predator-prey association which exists between these two species off Pt. Loma, California may be a regional phenomenon, since the relationship has not been reported from other localities along the Pacific Coast. However, from the responses in both laboratory and field situations we believe that the occurrence is probably more widespread than indicated in the literature. The large number (47%) of *S. purpuratus* we found included in the overall diets of leather stars off Pt. Loma, as opposed to the total exclusion of this species in the diets of leather stars off Washington state as reported by Mauzey et al. (1968) is extremely puzzling to us. We can only speculate at this time on what could account for this variation in feeding behavior. Selection of potential prey by *D. imbricata* may be determined by the following conditions: (1) Prey density and availability, (2) search time or the time required by the sea star to find and capture suitable prey, (3) taste or gustatory preferences of the sea star, and (4) some form of associative learning by *D. imbricata.*

Strongylocentrotus purpuratus appeared to be available to *D. imbricata* on almost a continuous basis within the study area, since the population of purple urchins was estimated to have a mean density value of 30.2/m^2. Predator search and capture time also seems to be related to the density and distribution patterns of the prey, as well as to the avoidance tactics employed by these potential prey. Encounters between the two species on uniform substratum usually resulted in the escape of *S. purpuratus;* however, when the purple urchins occupied depressions, holes, or crevices along the sea floor, they became more vulnerable to asteroid predation. In response to asteroid predation *S. purpuratus* has apparently evolved countermeasures such as evasive movement, and defensive utilization of spines and poisonous globiferous pedicellariae. The large number (90%) of feeding leather stars with purple urchin pedicellariae attached to their epidermis might lead one to suspect that these appendages are ineffective as a defensive mechanism. The pedicellariae, however, appear to act as an irritant that in certain situations halts the pursuit of a leather star and thus allows the urchin to escape. Marler and Hamilton (1966, p. 142) stated that "there is evidently a subtle and dynamic balance between these different evasive characteristics of the prey species on the one hand and the abilities of the predators to overcome them on the other". The taste or gustatory preferences of individual *D. imbricata* as compared to a leather star population has not been explored.

From our observations off Pt. Loma we would expect that at least a few purple urchins would show up in the diets of *D. imbricata* off Washington, even if other species were "preferred" above *S. purpuratus.* Possibly before leather stars prey on live urchins there is a learning

process involved before the sea star recognizes or associates specific stimuli with food. Tinbergen (1960) proposed that learning was involved in the feeding behavior of insect-eating birds, and that initial non-acceptance of specific insects by these birds was due to an unfamiliarity with these forms as prey. He further related initiation of feeding on a new food item with chance experience and prey density. Tinbergen (1960) suggested that the predator acquires a "specific search image" for the prey after being sufficiently impressed with it from frequent chance encounters. Holling (1958 and 1965) studied predation on the cocooned pupae of sawflies by shrews and mice, and suggested that associative learning was an important component in the feeding behavior of these small mammals.

Unfortunately, associative learning has been studied in only a relatively small number of lower animal (invertebrate) groups. Evans (1968) discussed this form of learning in cephalopods, insects, annelids, and flatworms. There is some evidence to suggest that associative learning exists in echinoderms. Landenberger (1966) found that the sea star *P. giganteus* learned to associate a light stimulus with food. The association apparently disappeared when the response to the light stimulus was no longer rewarded with food. If associative learning, with food as a reinforcement or reward, is a component in the feeding behavior of *D. imbricata*, then it might account for the presence of purple urchins in the diets of leather stars off Pt. Loma. This area contained a large number of highly accessible *S. purpuratus*, and yet at the same time appeared to be practically devoid of many of the sessile or sedentary invertebrates that these sea stars are reported to feed on. *Dermasterias imbricata* probably responds to a small class of chemical and/or tactile stimuli; however, only through associative learning and experience can it exploit an evasive prey species such as *S. purpuratus*. The leather star may not acquire the experience necessary to capture live *S. purpuratus* in other subtidal areas that contain alternate prey in greater abundance, since these forms are more accessible and possibly can account for the total nutrient requirements of *D. imbricata*.

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COMPARISON OF FOREGUT CONTENTS OF *Sergestes similis* OBTAINED FROM NET COLLECTIONS AND ALBACORE STOMACHS

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ABSTRACT

Sergestes similis, an oceanic shrimp, was taken at a number of locations in the eastern North Pacific, principally in the California Current region. The contents of foreguts from shrimp caught by net during the day and night and those of shrimp eaten by free-swimming fish were compared. In all three categories of foreguts the predominant prey were adult specimens of the larger, common calanoid copepods which typically inhabit the upper 200 to 300 m in the California Current region. However, because the diversity of calanoid species and the numbers of fish scales, calanoids, and euphausiids were appreciably greater in the foreguts of net-caught *S. similis* than in fish-caught samples, it appears likely that *S. similis* feeds in collecting nets under tow.

Sergestes similis Hansen is an abundant pelagic shrimp endemic to North Pacific waters of boreal-temperate influence (Pearcy and Forss, 1969; Judkins, unpublished data). Examination of its stomach contents indicates it is predaceous and feeds primarily on copepods and euphausiids (Renfro and Pearcy, 1966).

There is an expanding body of evidence that, in the freshwater environment, predation by planktivores is size selective and determines, in part, the composition of zooplankton communities (Brooks and Dodson, 1965; Brooks, 1968; Dodson, 1970; Hall, Cooper, and Werner, 1970). Size-selective feeding by an abundant oceanic carnivore such as *S. similis* may play an important role in limiting the abundance of an array of prey species within a size range and, hence, in determining the composition of the zooplankton community within its habitat. The first step in determining the impact of *S. similis* as a predator in the community is to identify and to enumerate the prey species it utilizes.

In this report we identify and enumerate the foregut contents of *S. similis* from net tows and albacore stomachs taken at a number of localities in the eastern North Pacific. To determine if the results were affected by feeding in the net or by diurnal changes in feeding intensity and diet, comparisons were made between three categories of specimens: day-net samples, night-net samples, and fish-stomach samples.

MATERIALS AND METHODS

About two thirds of the 270 foreguts with contents examined in this study were obtained from *S. similis* collected by nets, principally Isaacs-Kidd midwater trawls, over several seasons (Table 1). The remaining one third were obtained from troll-caught albacore taken in July-August 1968 (Laurs and Nishimoto, personal communication). With the exception of one net tow taken in the Gulf of California all of the collections were made in the northeast Pacific Ocean between lat 31° and 53° N (Table 1).

Carapace lengths (measured from the tip of the rostrum to the dorsal mid-point of the posterior margin) of the net-caught shrimp ranged from 6.5 to 17.0 mm, with a median of 11.3 mm. Carapace lengths of fish-caught shrimp ranged from 6.3 to 12.5 mm, with a median of 8.3 mm. Because many fish-caught shrimps were partially digested, it was necessary to estimate their carapace lengths from the lengths of their foreguts (Judkins, unpublished data).

The foreguts were removed intact from the specimens with fine forceps and placed on glass

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TABLE 1.—Material examined.

	Collection number	Gear	Date	Position		Time (local)	Depth	Sample size
				Latitude (N)	Longitude (W)		m	
Night-net	Northern Holiday 10	IKMT[1]	11 Aug. 1951	43° 08′	150° 00′	2130-2320	175	10
	CalCOFI 6204-H 60.60	IKMT	26-27 Mar. 1962	37° 37′	123° 37′	2024-0005	1,873	9
	60.90	IKMT	28 Mar. 1962	36° 34′	125° 46′	0012-0147	298	10
	80.55	IKMT	16 Mar. 1962	34° 18′	120° 48′	1930-2135	296	10
	80.60	IKMT	17 Mar. 1962	34° 07′	121° 08′	0100-0236	300	10
	100.40	IKMT	17 Apr. 1962	31° 21′	117° 27′	0229-0414	298	3
	Ursa Major 10	IKMT	16 Aug. 1964	47° 01′	155° 00′	0327-0416	245	10
	24-Shallow	BMOC[2]	28 Aug. 1964	47° 38′	155° 00′	2216-2238	100-75	4
	Fazor II Birch 4	Tucker T[3]	14 Feb. 1966	48° 12′	148° 37′	0622-0656	450	10
	MV 68-I-73	IKMT	20 Jan. 1968	29°	113°	2245-0507	1,000	10
	Total							86
Day-net	Northern Holiday 13	IKMT	18 Aug. 1951	53° 35′	146° 05′	1345-1655	450	6
	CalCOFI 6204-H 60.70	IKMT	27 Mar. 1962	37° 07′	124° 25′	0613-0750	298	4
	60.100	IKMT	28 Mar. 1962	36° 17′	126° 31′	0809-1226	1,863	3
	80.70	IKMT	17 Mar. 1962	33° 54′	121° 50′	0948-1424	1,863	5
	Ursa Major 25-Deep	BMOC	29 Aug. 1964	46° 15′	155° 02′	1640-1809	300-400	10
	Fazor II Birch 3	Tucker T	14 Feb. 1966	47° 54′	148° 23′	1519-1553	--	10
	SIO 67-101	IKMT	9 June 1967	35° 16′	122° 16′	0827-1534	2,200	10
	SIO 67-102	IKMT	10 June 1967	35° 19′	123° 06′	0705-1403	2,200	9
	SIO 67-113	IKMT	14 June 1967	37° 20′	123° 42′	0558-1150	2,200	8
	Total							65
Twilight-net	CalCOFI 6204-H 90.60	IKMT	6 Apr. 1962	32° 28′	120° 06′	0450-0620	148	10
	SIO 66-51	IKMT	21-22 May 1966	40° 35′	125° 52′	2003-0643	1,125	11
	SIO 67-47	IKMT	20 Apr. 1967	31° 36′	117° 54′	1508-1923	4,000	10
	Total							31
Fish stomachs	AO 68 Stomach 216	Troll	16 July 1968	~ 36°	~ 125°	1815		11
	233		17 July 1968	~ 34°	~ 124°	--		2
	241		18 July 1968	~ 35°	~ 126°	1213		24
	248		18 July 1968	~ 36°	~ 126°	1800		10
	92		19 July 1968	~ 39°	~ 127°	--		17
	179		20 July 1968	~ 42°	~ 127°	--		2
	140		21 July 1968	~ 44°	~ 127°	--		4
	58		2 Aug. 1968	~ 44°	~ 135°	--		5
	9		12 Aug. 1968	~ 45°	~ 124°	0555		15
	234		18 Aug. 1968	~ 36°	~ 125°	0615		10
	Total							100

[1] Isaacs and Kidd, 1953.
[2] McGowan and Brown, 1966.
[3] Tucker, 1951.

microscope slides where their contents were emptied into 100% glycerol. All observations were made with aid of a stereomicroscope or a compound microscope at various magnifications as needed from 16× to 1000×.

The contents were examined to identify and enumerate all particles. Several drops of lactic acid tinted with chlorozol Black E were added to the glycerol to facilitate identification of the components. Lactic acid aids in clearing the preparation. The tint stains the components and is especially useful for arthropod cuticle. The identity of crustacean prey was often established from the morphology of mandibles, genital segments, fifth legs, or other diagnostic features.

In Table 1, collection numbers grouped by the designation "night-net" represent a set of 10 samples varying in number from 3 to 10 shrimp each and collected by nets that were towed exclusively between sunset and sunrise. Collection

numbers designated "day-net" comprise a set of nine samples of from 3 to 10 shrimp each and collected by nets that were towed exclusively between sunrise and sunset. "Twilight-net" collection numbers represent three samples collected by nets which were actually towed at sunset or sunrise. Collection numbers designated "fish stomachs" represent 10 samples of 2 to 24 shrimp taken from stomachs of albacore. The albacore were taken during daylight hours by trolling lines; exact times of capture were not available for five of the specimens.

Included in statistical analyses were all classes of food occurring in 10% or more of any of the sets of night-net, day-net, and fish samples. Calanoid genera occurring in 10% or more of any of the sets of samples were considered separately. The small number of twilight-net samples was not included in statistical comparisons of the sampling categories, but the details of this set are given in Table 2. Overall means (no. prey/foregut) and frequencies (%) were calculated for the three sets of samples that were compared. In addition, means were calculated for each night-net, day-net, and fish sample. The Mann-Whitney *U*-Test, a test designed to estimate the significance of differences in median values of two samples was used to compare median sample means between day- and night-net samples and between combined day- and night-net samples and fish samples.

RESULTS

Ingested items included euphausiids, ostracods, amphipods, chaetognaths, and fish scales, but the principal identifiable components in all sampling categories were adult calanoid copepods (Table 2). The composition of foregut contents from different geographical regions (North Pacific Subarctic, North Pacific Drift, and the California Current) were very similar and hence were not considered separately. The diversity of calanoids was much greater in all categories of net samples than in fish samples: 42 species were identified in net samples, but only 7 were found in fish samples.

Foregut contents varied widely in the extent of maceration by digestion and mastication.

TABLE 2.—List of organisms and their frequency of occurrence in the foreguts of *Sergestes similis*.

	Night-net	Day-net	Twilight-net	Fish
Copepoda				
Aetidiopsis rostrata	4	--	--	--
Aetidiopsis	1	--	--	--
Aetidius	1	3	--	--
Calanus cristatus	--	--	1	--
Calanus pacificus	20	1	3	--
Calanus plumchrus	--	--	2	--
Calanus	18	9	3	--
Candacia bipinnata	--	--	2	10
Candacia	--	--	1	7
Chirudina	--	1	--	--
Clausocalanus furcatus	1	--	--	--
Clausocalanus parapergens	5	3	--	--
Clausocalanus	3	2	--	--
Corycaeus	1	--	--	--
Corycella	--	--	--	1
Eucalanus bungii	5	2	2	--
Eucalanus	4	5	--	--
Euchaeta propinqua	--	1	--	--
Euchaeta	8	7	4	1
Euchirella pulchra	1	2	--	--
Euchirella rostrata	--	1	1	--
Gaetanus	1	1	--	--
Gaidius pungens	2	1	--	--
Gaidius	4	3	--	--
Gaussia	2	--	--	--
Heterorhabdus abyssalis	2	1	2	--
Heterorhabdus	2	2	--	--
Lucicuta flavicornis	--	1	--	--
Lucicutia	--	--	1	--
Metridia brevicauda	--	1	--	--
Metridia pacifica	17	18	5	22
Metridia	20	11	--	2
Oncaea	3	1	2	1
Oithona	1	1	--	--
Paracalanus parvus	1	--	--	--
Paracalanus	4	--	--	--
Pareuchaeta	2	--	--	--
Phyllopus	--	1	--	--
Pleuromamma abdominalis	7	--	2	--
Pleuromamma borealis	1	1	1	1
Pleuromamma gracilis	2	--	--	--
Pleuromamma xiphias	1	1	1	--
Pleuromamma	11	6	4	1
Pseudocalanus	6	1	2	--
Rhincalanus nasutus	13	1	--	--
Rhincalanus	7	4	--	--
Racovitzanus	--	1	--	--
Scaphocalanus curtis	--	1	--	--
Scaphocalanus magnus	1	--	--	--
Scolecithricella abyssalis	--	--	1	--
Scolecithricella dentata	--	1	--	--
Scolecithricella minor	6	3	--	--
Scolecithricella ovata	3	1	--	--
Scolecithricella	--	3	1	--
Scottocalanus	1	--	--	--
Spinocalanus	1	2	--	--
Undeuchaeta intermedia	--	--	--	1
Undeuchaeta bispinosa	--	--	1	--
Undeuchaeta	2	--	--	1
unidentified calanoid	14	14	1	11
aegisthid harpacticoid	--	--	1	--
Euphausiacea				
Thysanoessa	12	--	--	--
unidentified	19	16	6	2
Ostracoda				
Conchaecia	--	2	--	1
unidentified	6	--	8	5
Amphipoda				
unidentified	5	9	--	6
Chaetognatha				
unidentified	12	1	--	2
Fish scales	17	16	3	--
Fish eggs	1	--	--	--
Foraminiferan, unidentified	--	2	--	--
Radiolarian, unidentified	--	1	--	1
Molluscan radula	1	--	1	--
Larvacean, unidentified	1	--	--	--
Cirriped cyprid	--	--	--	1
Unidentified debris	30	22	10	42
Total number foreguts with contents	86	65	31	58

Specimens in the same sample frequently varied from one another, and the degree of decomposition in each specimen usually was not uniform. Lightly digested prey were largely intact, and their internal organs still visible. Moderately digested prey contained obviously macerated tissue and were often incompletely fragmented. Prey in an advanced state were highly fragmented, and soft tissues were absent. Digestion of foregut contents tended to be less advanced in night-net than in day-net samples. However, most foreguts in both categories contained material in an advanced state of digestion.

Five groups of ingested material, calanoids, euphausiids, chaetognaths, fish scales, and unidentifiable matter, occurred in 10% or more of at least one of the three sampling categories (Figure 1). Unidentifiable material consisted primarily of crustacean fragments and matted aggregations of fibrous and granular debris. Of identifiable groups, calanoids were usually most abundant in all three categories (Table 3). The four identifiable groups of prey organisms appeared in higher numbers in net samples than in fish samples, differences between the median values, with the exception of chaetognaths, being significant at $P \leqslant 0.05$.

Frequencies, overall means, and median sample means of calanoids and euphausiids in day-net samples were less than were those in night-net samples. However, differences between the day and night median values of the four identifiable groups were not significant ($P > 0.50$). Twilight-net samples do not appear to differ appreciably from day- and night-net samples.

Calanoid genera occurring in more than 10% of the three categories (Figure 2) were *Metridia* (principally *pacifica*), *Calanus* (principally *pacificus*), *Pleuromamma* (principally *borealis*), *Rhincalanus* (all *nasutus*), *Euchaeta*, *Eucalanus* (principally *bungii*), *Scolecithricella*, and *Candacia* (principally *bipinnata*). These genera have been found typically in the uppermost 200 to 300 m of the California Current region (Fleminger, unpublished data).

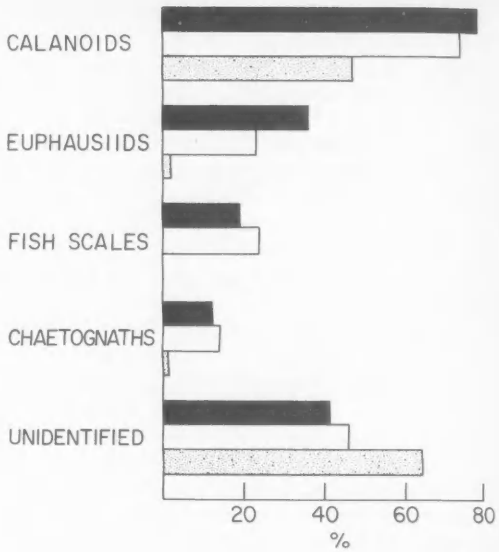

FIGURE 1.—Frequencies of ingested items occurring in 10% or more of night-net (black), day-net (open) and fish (strippled) samples.

The overall mean number of *Calanus* in day- and night-set samples are notably different (Table 4). In night-net samples *Calanus* ranked with *Metridia*, the two dominating the list of

TABLE 3.—Median of sample means and overall mean of number of prey per foregut.

Prey	Night-net			Day-net			Fish		
	Median	Range	Mean	Median	Range	Mean	Median	Range	Mean
Calanoids	2.40	0-12.50	4.23	2.25	0.67-5.70	2.68	0.63	0-3.20	0.96
Euphausiids	.33	0- 2.90	.66	.10	0-1.50	.32	0	0- .12	.02
Fish scales	.10	0- 1.00	.31	.23	0-3.00	.37	0		0
Chaetognaths	.20	0- .30	.15	.16	0- .33	.14	0	0- .50	.02
Number samples	10			9			10		
Total number foreguts	86			65			85		

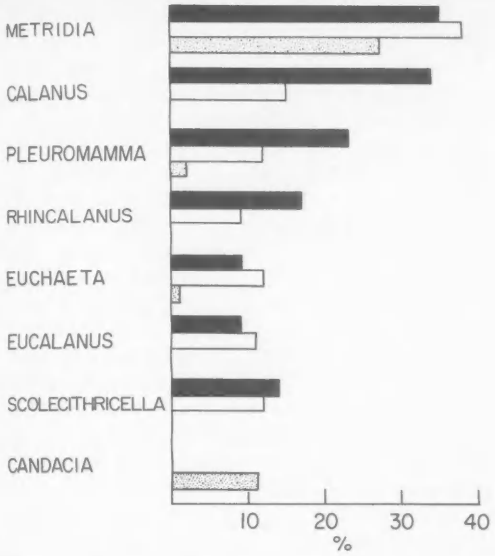

FIGURE 2.—Frequencies of calanoid genera occurring in 10% or more of night-net (black), day-net (open), and fish (strippled) samples.

calanoid prey. In day-net samples *Calanus* numbers are considerably below those of *Metridia* which remained high. However, the difference between the median sample means of *Calanus* in day- and night-net samples is not significant ($P > 0.20$). This is also true of the other seven genera.

Metridia was numerically dominant in fish samples, although it occurred in lower numbers than in net samples. Differences between the median sample means of *Metridia* in net and fish samples, however, are not significant ($P > 0.40$). Differences between net-and-fish-caught *S. similis* in the median values of *Eucalanus*, *Euchaeta*, and *Rhincalanus* are significant at P values falling between 0.10 and 0.20. Differences among the remaining calanoid genera are significant at P values between 0.02 and 0.10.

DISCUSSION

Metridia pacifica, *Calanus pacificus*, *Pleuromamma abdominalis*, *Rhincalanus nasutus*, *Eucalanus bungii californicus*, and *Candacia bipinnata* are among the 24 most abundant and frequently occurring of 176 calanoid species found in zooplankton samples collected on CalCOFI Cruises 5804, 5807, 5810, and 5901 (Fleminger, 1967). Significantly, these are also the principal species of six of the eight genera most frequently occurring in the foreguts examined in the present study. Adults of these species exceed 3 mm in length. It appears, then, that the principal prey of *S. similis* are the more abundant, relatively large, adult copepods inhabiting the uppermost 200 to 300 m in the California Current region.

Additional items found in both net and fish samples are euphausiids, chaetognaths, ostracods, amphipods, and radiolarians. Of these,

TABLE 4.—Median of sample means and overall mean in calanoid genera occurring in more than 10% of foreguts. [Means expressed as number of prey per foregut.]

Prey	Night-net			Day-net			Fish		
	Median	Range	Mean	Median	Range	Mean	Median	Range	Mean
Metridia	0.30	0-4.10	0.95	0.56	0-1.60	0.78	0.36	0-2.90	0.69
Calanus	.40	0-5.90	1.16	0	0- .80	.17	0		0
Pleuromamma	.30	0-1.10	.36	.10	0- .80	.15	0	0- .09	.02
Rhincalanus	.20	0-2.00	.35	0	0- .30	.09	0		0
Euchaeta	.10	0- .20	.10	0	0- .40	.14	0	0- .06	.01
Eucalanus	0	0- .30	.10	0	0- .50	.11	0		0
Scolecithricella	.10	0- .40	.13	.10	0- .30	.12	0		0
Candacia	0		0	0		0	.10	0- .50	.11
Number samples	10			10			10		
Total number foreguts	86			65			88		

only euphausiids were reported in a previous study on the diet of *S. similis* (Renfro and Pearcy, 1966).

A large percentage of shrimp of all sampling categories contained mixtures of granular and fibrous debris. The unidentifiable state of this material may not be entirely the result of digestive processes, but of the decomposed nature of the material at the time of its ingestion. *Sergestes similis*, like *S. lucens* (Omori, 1969), may scavenge decomposing dead material in addition to taking living prey. Another possibility is that this material represents the remains of prey stomach contents, e.g., those of euphausiids.

There is a tendency for day-net overall means to be less than those of night-net samples (Table 3). This and the trend toward less advanced digestion in night-net samples suggest more intense feeding activity at night, as was reported for *S. lucens* (Omori, 1969). The lesser average number of calanoids per foregut in day-net samples may be attributed primarily to the notably fewer *Calanus* in that category (Table 4).

Although the median values are not statistically different, day and night differences in overall mean numbers of the two calanoid species most frequently occurring in net samples, *Metridia pacifica* and *Calanus pacificus*, are notable in that they agree with differences in the vertical distributions of these two species. In the California Current region south of lat 33° N, *Calanus pacificus* usually concentrates in and near the thermocline during the day and disperses throughout the mixed layer at night. *M. pacifica*, on the other hand, occurs in the vicinity of the thermocline at night and disperses downward during the day (Fleminger, unpublished data). Studies have shown *S. similis* to be concentrated between the surface and 200 m at night and between 250 and 500 m during the day (Barham, 1957; Pearcy and Forss, 1966). The diurnal vertical range of *M. pacifica*, then, seems to correspond more closely with that of *S. similis* than does the diurnal range of *C. pacificus*. *Sergestes similis* probably has access to quantities of *M. pacifica* during both day and night. Most likely, *S. similis* encounters and feeds upon concentrations of *C. pacificus* primarily at night after the sergestid has ascended to shallower depths. However, without knowledge of digestive rates, these considerations are speculative.

The large numbers of fish scales in net samples and their complete absence in fish-stomach samples strongly suggest that feeding in the net has occurred. Although the source of these scales cannot be ascertained, it seems probable that they are the highly deciduous scales of lanternfish captured in the net with the shrimp. The significantly greater numbers of euphausiids and chaetognaths and the higher diversity of calanoids in net samples may also be indicative of feeding after capture. Many preserved net-caught *S. similis* have been observed by one of us (Judkins) to have fish scales, chaetognaths, and small crustaceans packed into their mouthparts and sometimes gripped in their mandibles.

Special conditions under which fish-caught shrimp might have been feeding before capture (related perhaps to time or depth) may also have contributed to the observed disparities between net and fish samples. Albacore are thought to feed primarily during daylight hours and probably most intensively in the early morning and early evening (Iversen, 1962). Time of capture by trolling of the albacore that we examined is available for only about half of the specimens. Of these about half were taken in morning daylight hours and the remainder were from the late afternoon and early evening. If all of the fish-caught shrimp were captured during the day, the relatively small quantities of identifiable components might reflect less intensive feeding by the shrimp at the time they were ingested by the albacore.

The generally smaller size of fish-caught specimens is probably not a factor; small net-caught shrimp (carapace length less than 10 mm) contained numbers of fish scales, euphausiids, and chaetognaths proportionally as high as larger net-caught individuals. Differences amongst sergestid specimens in the length of time spent in an albacore stomach also appear to be a negligible factor. Foregut contents of nearly intact fish-caught shrimp do not differ appreciably from those of extensively decomposed shrimp.

In general, the various samples of foreguts from adult *S. similis* that were analyzed provide

vide a coherent pattern of prey organisms consisting principally of the larger, commoner species of calanoid copepods inhabiting the uppermost 200 to 300 m of the California Current region. However, it is likely that feeding by *S. similis* in the net while it is being towed may explain the greater number and diversity of prey items in net-caught shrimp.

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NOTE

LONGEVITY AND GROWTH OF TAGGED KING CRABS IN THE EASTERN BERING SEA

During the period 1957 through 1959, the Bureau of Commercial Fisheries (now the National Marine Fisheries Service) released 32,328 tagged king crabs, *Paralithodes camtschatica*, in the eastern Bering Sea. Since then several thousands have been recovered, 23 of which exceed previously reported maximum ages for this species (Table 1). These crabs were originally captured by Bureau research vessels, marked with serially numbered plastic spaghetti tags inserted through the isthmal muscle (method described in Alaska Fisheries Board and Alaska Department of Fisheries, 1955: 34-43), and released immediately. Crabs were recaptured by the crab tangle net fisheries of Japan and the Soviet Union, and recapture data were provided by the two nations as part of annual exchanges of scientific information called for by bilateral fishing agreements with the United States.

We estimated the ages of the crabs at release from size and age data for young king crabs published by Weber (1967). Weber found that both male and female king crabs in the eastern Bering Sea mature at about 95 mm carapace length; that males reach this size in 5 years and females in 5½ years (assuming a hatching date of late April to early May); and that immature crabs longer than 60 mm increased about 16 mm per molt. Growth curves for both sexes were similar up to the fourth year of life (length of 80 mm), but after the females become mature they grow slower. The males, however, continue to grow about 16 mm per molt throughout the rest of their lives (Weber and Miyahara, 1962; Hoopes and Greenough, 1970).

Total age was estimated for all four males, and length data are available for three of the four (Table 1). One male released in 1957 was recaptured in 1968, having been at liberty for 11 years. This crab was estimated to have been 6 years old at time of release, and if this estimate is correct, it was 17 years old at time of recapture. If the average growth per molt was 16 mm, this crab molted three or four times during the 11 years between release and recovery, and the other two crabs for which growth data are available molted only once or twice in 9 years. This molting frequency is much lower than that reported by Weber and Miyahara (1962), but we have no explanation for the reduced rate of molting in the two crabs. Before this study, the oldest known-age king crab reported in the literature was a male that was tagged near Kodiak Island and recaptured 20 miles from the release location 6 years and 4 months later (Powell, 1965). Powell estimated that this male was 7 years old when tagged and 13 years old when recaptured.

TABLE 1.—Carapace lengths and estimated ages of 4 male and 19 female king crabs tagged in the eastern Bering Sea by the National Marine Fisheries Service in 1957, 1958, and 1959 and recovered 1966, 1968, and 1969.

Sex and tag no.	Release date	Recovery date	Carapace length at—		Estimated age at—	
			Release	Recovery	Release	Recovery
Males			mm	mm	*years*	*years*
B5178	9/9/57	9/16/68	108	170	6	17
B7013	4/29/58	5/18/66	124	[1]	7	15
B7364	5/2/58	3/30/68	109	132	6	15
C8909	5/14/59	9/25/68	108	133	6	15
Females						
B7535	5/3/58	5/21/68	97	138	5	15
B7560	5/3/58	6/26/68	94	152	5	15
B7567	5/3/58	6/8/69	99	149	5	16
B7906	5/4/58	5/10/66	109	[1]	6	14
B8008	5/4/58	4/30/68	110	155	6	15
B8015	5/4/58	5/18/66	108	[1]	6	14
B8552	5/11/58	3/28/69	108	149	6	16
B9150	5/26/58	5/8/69	90	138	5	15
C2111	6/17/58	5/8/69	130	162	8	18
C2508	6/17/58	4/30/68	99	140	5	14
C2561	6/17/58	6/21/68	114	157	7	17
C2785	6/17/58	5/9/68	77	136	4	13
C2804	6/17/58	5/20/68	108	150	6	15
C3871	6/27/58	5/5/68	97	162	5	14
C3969	6/27/58	5/19/68	94	147	5	14
C4106	6/27/58	6/14/68	107	137	6	15
C4423	6/28/58	3/29/68	104	141	6	15
C4837	6/29/58	9/1/69	102	136	5	16
C5961	7/5/58	5/17/68	91	120	5	14

[1] Not available.

Length and age data are available for 17 of the 19 females (Table 1). One attained an estimated age of 18 years, having been at liberty for 10 years after being tagged. If these 17 females molted once each year, their growth per molt ranged from 3.1 to 7.2 mm (length); the average increment was 4.7 mm. This average value is similar to other reported annual growth increments for female king crabs in Alaska waters—4.4 mm (Powell, 1967), 3.9 mm (Gray, 1963), 5.0 mm (Bright, Durham, and Knudsen, 1960), and 4.0 mm (Sakuda, 1959).

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